

FRAGMENT SIZE AND DENSITY EFFECTS ON THE GROWTH AND SURVIVAL
OF *MONTIPORA CAPITATA*.

A THESIS SUBMITTED FOR PARTIAL FULFILMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
BACHELOR OF SCIENCE

IN
GLOBAL ENVIRONMENTAL SCIENCE

May 2023

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I certify that I have read this thesis and that in my opinion, it is satisfactory in scope and quality as a thesis for the degree of Bachelor of Science in Global Environmental Science.

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ACKNOWLEDGEMENTS

I would like to first off thank Dr. Robert Toonen for advising me through this project. His willingness to share his knowledge within this field as well as go above and beyond to help guide me especially in the writing of this has not gone unnoticed. The suggestions Dr. Toonen has given me throughout this project has not only made this project a success but has also given me an opportunity to experience the efforts required to conduct and write an undergraduate thesis.

I would also like to thank Claire Lewis and Christopher Suchocki. Claire, for teaching me how to use the computer language R, which was used for all my data analysis. Without your help and guidance, I would have taken forever to configure a functioning code. Christopher, for helping me find my project, spending hours in the water helping me to collect data, and even to the last section of providing me edits on my writing. You were with me all the way throughout.

Lastly, I would like to thank Claire Bardin for helping collect data week after week, in rain or shine. Regardless of the conditions her positive energy and humor made it such a fun and enjoyable experience.

ABSTRACT

We compared the effects of fragment size and density on the growth rate of the coral *Montipora capitata* following micro fragmentation. Squares of 1, 2, or 3 cm per side were cut from a single colony of *M. capitata* to create small (1 cm²), medium (4 cm²), and large (9 cm²) fragments. Two to six fragments of each of these size classes were glued to a tile in a grid with 3 cm spacing between each fragment to create either high- or low-density treatments. Tiles were grown in a midwater coral nursery in Kāneʻohe Bay for 8 months to observe the effect of size and density on growth and survival of fragments. Small fragments died at a significantly higher rate than large fragments, and medium fragments were intermediate in numeric value and significance. Further, many of the surviving small fragments lost tissue, resulting in negative median growth, which was offset to positive mean growth overall by a small number of quickly growing fragments. There was no significant effect of either size class or density on percent increase in coral cover (growth) throughout the experiment. There are logistical reasons to recommend medium fragments at low density to reduce coral mortality relative to the smallest fragments, and still benefit from the higher growth rate relative to the largest fragments. Therefore, we conclude that medium sized fragments at low density is the best compromise for coral restoration activities using *Montipora capitata*.

Keywords: coral fragmentation, coral survivorship, coral growth

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CHAPTER 1 INTRODUCTION

Coral reefs occupy only ~0.2% of the seafloor but are home to more than 25% of ocean biodiversity (Knowlton et al., 2010; Komyakova et al., 2013). Corals help shape coastal ecosystems, providing sources of food for marine predators and humans. Corals create complex three-dimensional structures that both create habitat for other marine organisms and change the way water moves and waves break (Graham & Nash, 2013; Elliff & Silva, 2017). Globally, the health of coral reefs is in decline due to the combined effects of humans on our coastal waters, including increased carbon emissions leading to ocean warming and acidification (Hughes et al., 2003; Munday et al., 2008; Pandolfi et al., 2011).

Corals are animals that live in symbiosis with an endosymbiotic dinoflagellate that photosynthesizes and fixes carbon (Muscatine & Porter, 1977). These symbionts, also known as zooxanthellae (family Symbiodiniaceae), live within the coral's endoderm and provide corals with up to 90% of their daily energy requirements (Muscatine & Porter, 1977). Marine heatwaves are a major threat to coral reefs because they can cause breakdown of that symbiosis when zooxanthellae leave or are expelled by the coral host (Brown, 1997; Douglas, 2003; Jokiel, 2004). Due to the lack of symbiotic algae, the coral tissue becomes transparent enough to see the white skeleton beneath, which results in the bleached appearance. Additional impacts of climate change on corals include more frequent and powerful tropical storms that cause physical damage to the reef (Harmelin-Vivien, 1994; Rinkevich, 1995; Madin et al., 2012; Pörtner et al., 2022). As both natural and anthropogenic phenomena increasingly impact the ability of coral reefs to grow and

recover, half of the world's coral reefs have already been lost and many more are under increasing threat (Cesar et al., 2003; Eddy et al., 2021; Souter et al., 2021; Settler et al., 2022).

Hawai'i is known as an optimal location for coral growth and survivorship due to clear and warm surface waters (Hoegh-Guldberg et al., 2017). However, sea surface temperature in Hawai'i is increasing (Jokiel and Brown, 2004). Long periods of elevated ocean temperatures have triggered massive bleaching events in Hawai'i (Jokiel and Brown, 2004; Jury and Toonen, 2019). Kaneohe Bay is a site of extensive research for coral response and adaptation to the changing environment (Bahr et al., 2015). Corals in Kāne'ohe Bay have encountered challenging environmental conditions, such as consecutive bleaching events in 2014 and 2015, (Wall et al., 2021) as well as anthropogenic disturbances through dredging, clearing out land for agriculture resulting in increased sedimentation, and sewage discharge from 1930 through 1975 (Bahr et al., 2015). Studies have shown that corals in Hawai'i can adapt to changing conditions (Coles et al., 2018; Jury and Toonen, 2019). Yet, coral reefs in Hawai'i are still expected to face mass mortality as well as reduced calcification rates by the end of the century (Hoeke et al., 2011). Increased research is desired to better understand coral response to changing conditions as well as solutions to declining reef health (Wall et al., 2021).

As the loss of coral reefs continues and the situation becomes more dire, people have been galvanized to communicate the plight of coral reefs (Chasing Coral, 2017) and pursue human interventions that seek to conserve reefs across the planet (van Oppen et al. 2015). Solutions such as reducing carbon emissions are unlikely to be resolved before coral reefs are decimated (De'ath et al., 2012; Zhao et al., 2022; but see Timmers et al.,

2021; Jury et al., 2021). A proposed solution to reversing the loss of coral reefs is to seek methods of active restoration in which corals can be cultured and out planted to make up for extensive coral reef loss (Rinkevich, 1995; reviewed by Boström-Einarsson et al. 2020). One of the most widely used methods to produce corals for restoration is asexual replication of colonies through coral micro-fragmentation (Forsman et al. 2015; Page et al. 2018; Tortolero-Langarica et al. 2020; Knapp et al. 2022). The rate at which corals grow is extremely variable (Soper et al., 2022) and the vast majority of restoration to date has focused on fastest-growing corals (Boström-Einarsson et al. 2020). However, reefs include a diversity of fast and slow-growing species, and micro-fragmentation is the only method by which to produce slow-growing massive corals on a reasonable time scale (Forsman et al. 2015; Page et al. 2018).

In response to growing demands for coral restoration, the National Academies of Sciences, Engineering and Medicine recently released two reports (NASEM 2019a,b) that are being used as a roadmap by many across the globe for applied conservation of coral reefs. Efforts to actively create coral reef habitats have spawned considerable research about methods and effectiveness of coral restoration (Forsman et al. 2018; Boström-Einarsson et al. 2020; Knapp et al. 2022). Here, we explore the effects of fragment size and density on the growth and survival of coral fragments in a nursery for restoration activities. These results will further our understanding of the optimal conditions for creating large coral colonies for out planting during restoration efforts.

CHAPTER 2 METHODS

2.1 Study System

We studied the reef-building species *Montipora capitata* Dana, 1846, also known as rice coral (Veron et al., 2016). This species is common in the Indo-Pacific and prefers shallow, turbulent waters: conditions often present in Hawai‘i (Grigg, 1998). Not only is *M. capitata* common in Hawai‘i, but this species plays a crucial role in building and maintaining Hawai‘i’s reefs (Franklin et al., 2013; Bahr et al., 2015). Fragments of *M. capitata* used in this experiment were from a single colony and sourced from the coral nursery at HIMB (Hawai‘i Institute of Marine Biology). Coral genotype is one of the major drivers of differences in coral growth and survival of outplants for restoration in Hawai‘i (Henley et al. 2022; Knapp et al. 2022). Thus, using a coral with the identical genetic makeup (clonal ramets from the same colony) here controlled for individual genetic variation.

We conducted the experiment in the midwater coral nursery of the University of Hawai‘i at Mānoa’s Hawai‘i Institute of Marine Biology, on Moku o Lo‘e (commonly known as Coconut Island) located within Kāne‘ohe Bay on the island of O‘ahu (Figures 1 and 2).



Figure 1: Google Maps imagery showing the location of Hawai'i Institute of Marine Biology's coral nursery (project site).



Figure 2: Experimental location, the Hawai'i Institute of Marine Biology coral nursery.
PC: Jasmine Awaya.

2.2 Experimental Design

To ensure that each fragment had a tissue area of 1 cm², 4 cm², or 9 cm², guides were made by measuring squares of each respective size on a waterproof paper. Using a Gryphon Diamond Band Saw Model C-40 (Gryphon Corporation, CA) the single *M. capitata* colony was cut to the size classes, and additional cuts to shave off the skeleton were made to create a flat surface to allow for maximum adhesion between the *Montipora capitata* fragments and the ceramic tile. We then glued the fragments on a terracotta tile that measured 15.24 cm² using Extra Thick Super Glue Gel (Bulk Reef Supply, Golden Valley, MN) to create the size and density treatments. The independent variables in this experiment were the size (small, medium, or large) and density (low or high) of the coral fragments. Each tile included a label that was mounted using the same super glue used to mount the *M. capitata* fragments. Within each size class, high- and low-density treatments were created by maximizing the number of fragments on each tile while maintaining a constant spacing of 3 cm between each fragment (Figure 3). There was a total of 60 terracotta tiles, each size class (small, medium, and large) had 20 tiles each, and within each size class 10 terracotta tiles were for either high- or low-density treatments.

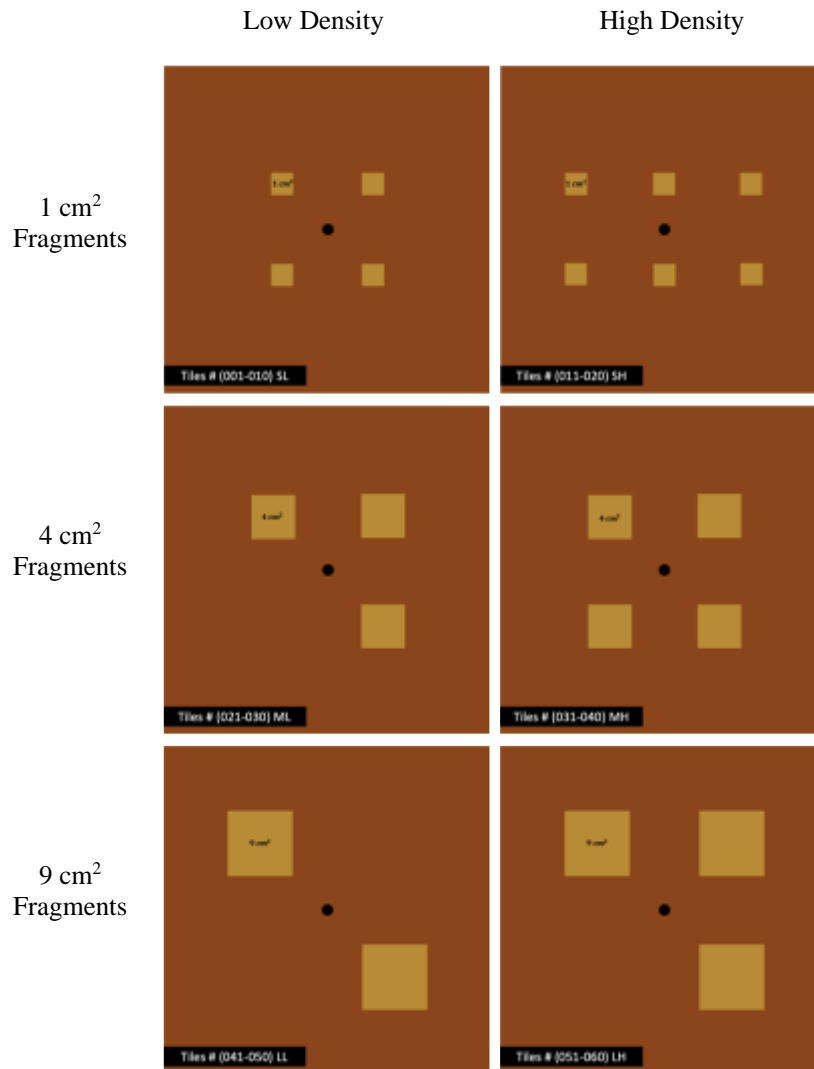


Figure 3: Digital layout of the terracotta tile with the corresponding *Montipora capitata* fragments for the 6 different treatments studied in this experiment. Small fragments measured 1cm by 1cm (1 cm²), medium measured 2cm by 2cm (4 cm²), and large measured 3cm by 3cm (9 cm²) that were then attached in either low- or high-density.

All 60 tiles were housed on a 1.52 m² rack with a buoy attached to each corner, allowing it to float about 1.52 meters below the surface of the water. The rack was constructed out of 1” Schedule 40 PVC pipe with intersecting pipes across the middle for support. Geomesh was laid over top of the PVC pipe frame where the tiles were placed

on top. The intersecting PVC pipes in the middle created a quadrant design, 15 tiles were placed in every quadrant in 3 rows of 4 tiles and 1 row of 3 tiles. Once the tiles were assembled, photographs were taken of each tile from a bird's eye view with a Sony A7 III camera that was set on a mount allowing for a constant distance between the tile and camera lens, preventing changes in either the distance or angle of the photograph (Figure 4). A color scale and ruler were included in each photograph to help determine the color scale and size scale of the *Montipora capitata* fragments. Photos were taken in shaded conditions inside the HIMB nursery shack to prevent harsh and variable lighting that may make digital analysis difficult. Photographs of the tiles were taken approximately once a month over the course of about 8 months and used for growth measurements.



Figure 4: A birds eye view photo of tile, ruler, and color pallet. A photo of each tile was taken in the same layout using a Sony A7 III, which would later be used to gather growth data. PC: Christopher Suchocki

2.3 Data Collection

Once initially photographed in November 2021, the tiles were placed onto the PVC rack for a 2-week acclimatization period, which allowed corals to recover from the stress of being cut and glued to the terracotta tiles. Observations of survivorship were made on a weekly basis during and after the acclimatization period. After the 2-week acclimatization, tiles were re-randomized on the PVC rack. Survival was determined by visual observations on a weekly basis. If any live tissue was present on the fragment, it was considered alive, whereas fragments with no visible live tissue were scored as dead. All fragments on a tile must have died before the treatment was no longer considered as alive. Once the experiment was concluded in June 2022, we then started data analysis. We first ran a 2-way ANOVA in R version 2022.02.3 to test statistical significance of size class and density on survival and total growth. Post-hoc pairwise comparisons allowed us to test for differences between treatments.

Growth was measured digitally using ImageJ. Area measurements of each individual fragment were taken for each tile monthly. The difference between the final and initial live area on each tile was calculated and was used to derive growth (the total percent change of coral cover on the tile). If all fragments were dead on a tile, then it was removed from the analyses. We used a 1-way ANOVA to test the statistical significance of either size class or density on percent change in growth or survivability. A 2-way ANOVA tested the statistical significance of size class and density on percent change in growth or survivability. Post-hoc pairwise comparisons were also used to determine differences in treatments.

CHAPTER 3 RESULTS

Size class of fragments had a significant impact (ANOVA: $df = 2$, $F = 4.8$, $P = 0.01$) on survival of coral fragments (Figure. 5A). The large (9cm^2) fragments had the greatest mean survivorship ($\bar{x} = 68.4 \pm 27.4\%$) compared to the small (1cm^2) fragments with the lowest mean survivorship ($\bar{x} = 38.8 \pm 29.1\%$), which is significant in a pairwise comparison ($P = 0.01$). Mean survival of medium fragments ($\bar{x} = 58.8 \pm 33.0\%$) was lower than mean survival of larger fragments ($\bar{x} = 68.4 \pm 27.4\%$), but these differences were not significant in a pairwise comparison ($P = 0.33$). Both the mean and median survival of small fragments was substantially lower than that of medium fragments, although this difference is not significant ($P = 0.09$, Figure. 5A).

In contrast to survival, size class had no significant effect on growth of coral fragments (ANOVA: $df = 2$, $F = 0.5$, $P = 0.59$; Fig. 5B), and none of the pairwise comparisons were significant. Small fragments showed the lowest overall increase in coral cover ($\bar{x} = 0.41 \pm 51.0\%$), followed by the medium fragments ($\bar{x} = 9.5 \pm 44.6\%$), and the large fragments showed the greatest growth ($\bar{x} = 15.2 \pm 31.3\%$) throughout this experiment. Interestingly, the mean growth of small fragments is positive, but the median growth is negative (-16.23%), unlike the medium and large fragments which showed overall positive growth (Figure 5B). The positive mean growth, yet negative median growth for the small fragments resulted from the majority of these fragments declining during the experiment, even though a few individuals showed high enough growth to increase the mean (0.41%) above the median (-16.23%).

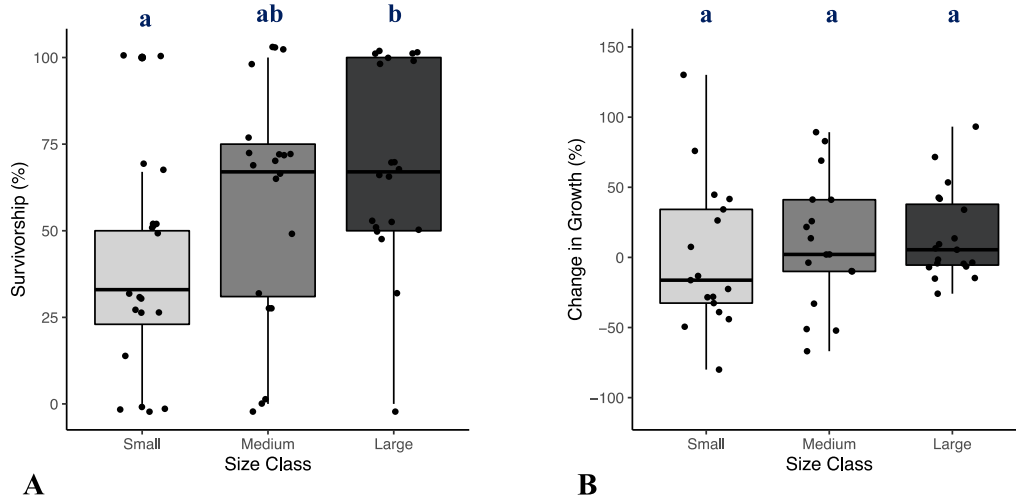


Figure 5: Box and whisker plots of growth and survival of *M. capitata* of differing sizes. (A) Percent survivorship of fragments cut to each size class ($S = 1 \text{ cm}^2$, $M = 4 \text{ cm}^2$, $L = 9 \text{ cm}^2$) throughout the experiment. (B) Growth (measured as percent change) of surviving coral fragments throughout the experiment. Small blue letters indicate statistically significant groups from post-hoc pairwise tests ($P < 0.05$).

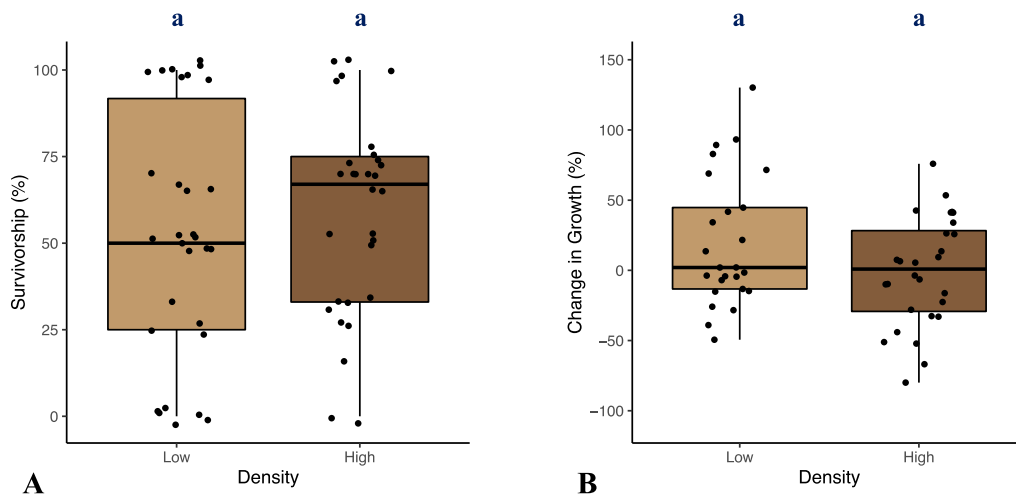


Figure 6: Box and whisker plots of growth and survival of *M. capitata* of differing density. (A) Percent survivorship of *M. capitata* fragments based on low- and high-density treatments throughout the experiment. (B) Growth (measured as percent change) of surviving coral fragments between low- and high-density treatments throughout the experiment. Small blue letters indicate statistically significant groups from post-hoc pairwise tests ($p < 0.05$).

Density had no significant relationship on survival of coral fragments (ANOVA: $df = 1$, $F = 0.49$, $P = 0.49$). The percent survivorship of the low-density tiles ($\bar{x} = 54.5 \pm 35.7$) were not different than that of the high-density tiles ($\bar{x} = 58.1 \pm 28.4$), although the median survivorship of the high-density fragments is 67% compared to 50% in the low-density trials. Similarly, density had no significant effect on growth overall (ANOVA: $df = 1$, $F = 2.8$, $P = 0.10$), and a pairwise comparison confirms that growth rates were not significantly different between treatments ($P = 0.08$). Overall, growth in the low-density treatments was positive ($\bar{x} = 19.6 \pm 45.8$) whereas growth in the high-density treatments ($\bar{x} = -1.1 \pm 38.0$) was negative, although the median values for each treatment are very close to zero (Figure. 6).

The combination of size class and density did not have a significant effect on percent survivorship (2-way ANOVA: $df = 2$, $F = 1.139$, $P = 0.33$), although size class alone did ($P = 0.01$). Similarly, when looking at the effect of size class and density on growth, there was no significant relationship (2-way ANOVA: $df = 2$, $F = 1.609$, $P = 0.21$), and no significant effect of the factors individually either ($P = 0.59$).

CHAPTER 4 DISCUSSION

The loss of more than half of coral reefs on the planet since the 1950s, and continued decline of coral reef ecosystems today, is of considerable global concern (Pandolfi et al. 2003; Eddy et al., 2021; Souter et al., 2021; Settler et al., 2022). Nearly a billion people rely on coral reef ecosystems as a significant source of food, and in addition to their intrinsic biological and cultural value, the annual economic benefits of marine ecosystem services have been reduced by an estimated \$10.9 trillion USD per year due primarily to the loss of coral reefs (Costanza et al. 2014). The continued loss of coral reefs despite global conservation efforts has resulted in a surge of research and activities focused on active coral restoration and rehabilitation of degraded coral reefs that no longer provide the desired ecosystem services (Anthony et al. 2020; Boström-Einarsson et al. 2020; Kleypas et al. 2021). Restoring a functional coral reef at a scale that provides such ecosystem services is a daunting task that faces many challenges but may be the only viable path remaining for some highly degraded former reef sites (Lirman & Schopmeyer 2016; Fox et al. 2019; Knowlton et al. 2021). Efforts to captively propagate corals for reef restoration and rehabilitation have evolved quickly from the early beginnings of live coral husbandry to coral production at scales required to outplant tens of thousands of colonies needed to produce a functional coral reef (Delbeek 2001; Young et al. 2012; Leal et al. 2016; Barton et al. 2017). While considerable advances have been made in this regard, the field of research is relatively new, and many basic questions about maximizing production of coral with minimal impacts on healthy reefs in the wild (Forsman et al. 2018; Boström-Einarsson et al. 2020; Knapp et al. 2022).

Here, we explored the effects of fragment size and density on the growth and survival of fragments of the rice coral *M. capitata*, which is a common species being targeted for restoration activities in Hawai'i. We found that size class of the fragments had a significant effect on total survivability. Large fragments (3cm x 3cm) had the greatest mean survival (68.4%), and the smallest fragments (1cm x 1cm) had the lowest mean survival (38.8%). We hypothesize that the initial stress placed on the fragment, with smaller fragments having greater proportional damage to the colony relative to the amount of live tissue from which to draw resources to heal and resume growth when compared to larger fragments (Anthony et al., 2002), made recovery more challenging. Additionally, smaller fragments are easier for predators to consume (Bruckner et al., 2000), and we know fish grazing was occurring as evidenced by bite marks and entire fragments being lost from the tiles. Along with survivorship being lowest in the smallest size class, the majority of small fragments that survived still showed some tissue loss (negative growth) such that the median growth rate in the experiment is roughly -16%. However, the mean growth remained positive (0.4%), because those small fragments that survived and showed positive growth had the highest proportional increase of any in the experiment.

Although the survival of medium fragments was closer to that of the large than the small fragments, the low sample size used in this experiment likely explains why this difference is not significant. It is likely that a larger experiment with greater sample size would make this trend more significant. Similarly, we saw no differences in the proportional growth of fragments by size class, suggesting that percent increase among each fragment remains relatively similar regardless of the size class treatments. This

result suggests that there is a trade-off between minimizing fragmentation stress by preserving larger portions of intact tissue and maximizing growth by getting the highest proportion of edge material that can actively grow. Thus, the medium fragments appear to be the best option in terms of both growth and survival in these experiments (Fig 5).

In contrast, density had no significant impact on either growth or survival of fragments. None of the fragments in this experiment grew to the point where they fused and formed a single continuous colony, which is one of the proposed benefits of micro fragmentation (Forsman et al. 2015; Page et al. 2018). If the metric for this trial was the time needed to completely cover the tile with live coral, and if we ran the experiment long enough to reach that endpoint, we would expect higher density treatments to grow over the tile faster than low density trials. However, the trade off with density comes in terms of the amount of healthy coral tissue needed for a project, the cost of materials, and labor to attach those fragments. From this experiment it seems that there is no benefit to the increased labor and coral starting material required to create the high-density trials. If anything, the low-density trials seem to perform slightly better because there is a slight increase in both the mean growth and survival of low-density fragments, although they are not significantly different from one another (Figure 6). Again, a larger sample size might have overcome the high individual variability, even though all fragments originated from the same initial colony, potentially making this effect significant.

Finally, we see no interaction between fragment size and density in this experiment. This result is promising because it means we can consider each factor independently for optimization of coral micro fragmentation techniques. Given the results of this experiment, we do not expect complex interactions between size class and density

that would complicate the design of coral restoration activities for *M. capitata*.

Survivorship and growth results were agreeable with the results received in the Knapp et al., 2022 experiment. In the Knapp et al., 2022 experiment the lowest survivorship was observed with the small fragments. Similarly, in the Knapp et al., 2022 experiment growth rates for individual treatments were variable.

CHAPTER 5 CONCLUSION

This study provided important information about the role of micro fragmentation as a restoration process to propagate *M. capitata* in Hawai'i. Taken together, these results indicate that the gains of growth seen from fragmenting corals to the smallest size class are offset by the partial and complete mortality of those small fragments. Smallest fragments may have the greatest potential for growth but also show the highest mortality rates, whereas larger fragments show the highest survival, but require substantially more starting material for an equivalent number of fragments. Overall, it seems that the medium sized fragments (2cm²) are the best compromise among the variables of starting material, growth potential, survivorship, and growth. Knowing this information, restoration efforts can maximize the probability of success without the need for more starting coral colonies, or the increased labor needed to cut and attach small fragments. We recommend medium fragments (on the order of 4 cm²) at low density as the best compromise for size and starting material used in coral restoration activities using *M. capitata*.

LITERATURE CITED

- Anthony, K. R., Connolly, S. R., & Willis, B. L. (2002). Comparative analysis of energy allocation to tissue and skeletal growth in corals. *Limnology and Oceanography*, *47*(5), 1417–1429. <https://doi.org/10.4319/lo.2002.47.5.1417>
- Anthony, K. R., Helmstedt, K. J., Bay, L. K., Fidelman, P., Hussey, K. E., Lundgren, P., Mead, D., McLeod, I. M., Mumby, P. J., Newlands, M., Schaffelke, B., Wilson, K. A., & Hardisty, P. E. (2020). Interventions to help coral reefs under global change—a complex decision challenge. *PLOS ONE*, *15*(8). <https://doi.org/10.1371/journal.pone.0236399>
- Bahr, K. D., Jokiel, P. L., & Toonen, R. J. (2015). The unnatural history of kāne‘ohe bay: Coral reef resilience in the face of centuries of anthropogenic impacts. *PeerJ*, *3*. <https://doi.org/10.7717/peerj.950>
- Barton, J. A., Willis, B. L., & Hutson, K. S. (2015). Coral propagation: A review of techniques for ornamental trade and reef restoration. *Reviews in Aquaculture*, *9*(3), 238–256. <https://doi.org/10.1111/raq.12135>
- Boström-Einarsson, L., Babcock, R. C., Bayraktarov, E., Ceccarelli, D., Cook, N., Ferse, S. C., Hancock, B., Harrison, P., Hein, M., Shaver, E., Smith, A., Suggett, D., Stewart-Sinclair, P. J., Vardi, T., & McLeod, I. M. (2020). Coral restoration – a systematic review of current methods, successes, failures and Future Directions. *PLOS ONE*, *15*(1). <https://doi.org/10.1371/journal.pone.0226631>
- Brown, B.E., 1997. Coral bleaching: causes and consequences. *Coral reefs*, *16*, pp.S129-S138.

Bruckner, A. W., Bruckner, R. J., & Sollins, P. (2000). Parrotfish predation on live coral: "Spot biting" and "focused biting". *Coral Reefs*, 19(1), 50–50.

<https://doi.org/10.1007/s003380050225>

Cesar, H., Burke, L. and Pet-Soede, L., 2003. The economics of worldwide coral reef degradation. Food & Agriculture Organization of the United Nations Special Report, 24 pp.

Chasing Coral [Film] (2017). Orłowski, J. (Director). Netflix.

<https://www.chasingcoral.com/https://www.youtube.com/watch?v=aGGBGcjdjXADe'at>

h, G., Fabricius, K. E., Sweatman, H., & Puotinen, M. (2012). The 27–year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National*

Academy of Sciences, 109(44), 17995–17999. <https://doi.org/10.1073/pnas.1208909109>

Coles, S. L., Bahr, K. D., Rodgers, K. S., May, S. L., McGowan, A. E., Tsang, A., Bumgarner, J., & Han, J. H. (2018). Evidence of acclimatization or adaptation in Hawaiian corals to higher ocean temperatures. *PeerJ*, 6. <https://doi.org/10.7717/peerj.5347>

Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderson, S. J., Kubiszewski, I., Farber, S., & Turner, R. K. (2014). Changes in the global value of Ecosystem Services. *Global Environmental Change*, 26, 152–158. <https://doi.org/10.1016/j.gloenvcha.2014.04.002>

Delbeek, J.C. Coral Farming: Past, Present and Future Trends. *Aquarium Sciences and Conservation* 3, 171–181 (2001). <https://doi.org/10.1023/A:1011306125934>

Douglas, A.E., 2003. Coral bleaching—how and why?. *Marine pollution bulletin*, 46(4), pp.385-392.

Eddy, T. D., Lam, V. W. Y., Reygondeau, G., Cisneros-Montemayor, A. M., Greer, K., Palomares, M. L., Bruno, J. F., Ota, Y., & Cheung, W. W. L. (2021). Global decline in capacity of coral reefs to provide ecosystem services. *One Earth*, 4(9), 1278–1285.
<https://doi.org/10.1016/j.oneear.2021.08.016>

Elliff, C.I. and Silva, I.R., 2017. Coral reefs as the first line of defense: Shoreline protection in face of climate change. *Marine environmental research*, 127, pp.148-154.

Forsman, Z. H., Page, C. A., Toonen, R. J., & Vaughan, D. (2015). Growing coral larger and faster: Micro-colony-fusion as a strategy for accelerating coral cover. *PeerJ*, 3.
<https://doi.org/10.7717/peerj.1313>

Forsman, Z. H., Maurin, P., Parry, M., Chung, A., Sartor, C., Hixon, M. A., Hughes, K., Rodgers, K., Knapp, I. S. S., Gulko, D. A., Franklin, E. C., Del Rio Torres, L., Chan, N. T., Wolke, C. S., Gates, R. D., & Toonen, R. J. (2018). The first Hawai‘i Workshop for Coral Restoration & Nurseries. *Marine Policy*, 96, 133–135.
<https://doi.org/10.1016/j.marpol.2018.08.009>

Fox, H. E., Harris, J. L., Darling, E. S., Ahmadi, G. N., Estradivari, & Razak, T. B. (2019). Rebuilding coral reefs: Success (and failure) 16 years after low-cost, low-tech restoration. *Restoration Ecology*. <https://doi.org/10.1111/rec.12935>

- Franklin, E. C., Jokiel, P. L., & Donahue, M. J. (2013). Predictive modeling of coral distribution and abundance in the hawaiian islands. *Marine Ecology Progress Series*, 481, 121–132. <https://doi.org/10.3354/meps10252>
- Graham, N.A. and Nash, K.L., 2013. The importance of structural complexity in coral reef ecosystems. *Coral reefs*, 32, pp.315-326.
- Grigg, R. W. (1998). Holocene coral reef accretion in Hawaii: A function of wave exposure and sea level history. *Coral Reefs*, 17(3), 263–272. <https://doi.org/10.1007/s003380050127>
- Harmelin-Vivien, M.L., 1994. The effects of storms and cyclones on coral reefs: a review. *Journal of Coastal Research*, pp.211-231.
- Helmkamp, M., Renee Bellinger, M., Geib, S. M., Sim, S. B., & Takabayashi, M. (2019). Draft genome of the Rice Coral *Montipora capitata* obtained from linked-read sequencing. *Genome Biology and Evolution*, 11(11), 3094–3094. <https://doi.org/10.1093/gbe/evz203>
- Henley, E. M., Bouwmeester, J., Jury, C. P., Toonen, R. J., Quinn, M., Lager, C. V. A., & Hagedorn, M. (2022). Growth and survival among Hawaiian corals outplanted from tanks to an ocean nursery are driven by individual genotype and species differences rather than preconditioning to thermal stress. *PeerJ*, 10. <https://doi.org/10.7717/peerj.13112>
- Hoegh-Guldberg, O., Poloczanska, E. S., Skirving, W., & Dove, S. (2017). Coral reef ecosystems under climate change and ocean acidification. *Frontiers in Marine Science*, 4. <https://doi.org/10.3389/fmars.2017.00158>

- Hoeke, R. K., Jokiel, P. L., Buddemeier, R. W., & Brainard, R. E. (2011). Projected changes to growth and mortality of Hawaiian corals over the next 100 years. *PloS one*, 6(3), e18038. <https://doi.org/10.1371/journal.pone.0018038>
- Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B., Kleypas, J. and Lough, J.M., 2003. Climate change, human impacts, and the resilience of coral reefs. *science*, 301(5635), pp.929-933.
- Jokiel, P.L., 2004. Temperature stress and coral bleaching. *Coral health and disease*, pp.401-425.
- Jury, C., Bahr, K., Barba, E., Brainard, R., Cros, A., Dobson, K., Graham, A., McLachlan, R., Nelson, C., Price, J., de Souza, M. R., Shizuru, L., Smith, C., Sparagon, W., Squair, C., Timmers, M., Tran, T., Vicente, J., Webb, M., ... Toonen, R. (2021). Experimental Reef communities persist under future ocean acidification and warming. <https://doi.org/10.21203/rs.3.rs-640089/v1>
- Kleypas, J., Allemand, D., Anthony, K., Baker, A. C., Beck, M. W., Hale, L. Z., Hilmi, N., Hoegh-Guldberg, O., Hughes, T., Kaufman, L., Kayanne, H., Magnan, A. K., Mcleod, E., Mumby, P., Palumbi, S., Richmond, R. H., Rinkevich, B., Steneck, R. S., Voolstra, C. R., ... Gattuso, J.-P. (2021). Designing a blueprint for Coral Reef Survival. *Biological Conservation*, 257, 109107. <https://doi.org/10.1016/j.biocon.2021.109107>
- Knapp, I. S. S., Forsman, Z. H., Greene, A., Johnston, E. C., Bardin, C. E., Chan, N., Wolke, C., Gulko, D., & Toonen, R. J. (2022). Coral micro-fragmentation assays for optimizing active reef restoration efforts. *PeerJ*, 10. <https://doi.org/10.7717/peerj.13653>

Knowlton, N., Brainard, R.E., Fisher, R., Moews, M., Plaisance, L. and Caley, M.J., 2010. Coral reef biodiversity. *Life in the world's oceans: diversity distribution and abundance*, pp.65-74.

Knowlton, N., Corcoran, E., Felis, T., Ferse, S., de Goeij, J., Grottoli, A., Harding, S., Kleypas, J., Mayfield, A., Miller, M., Obura, D., Osuka, K., Peixoto, R., Randall, C., Voolstra, C., Wells, S., & Wild, C. (2021). Rebuilding coral reefs: A decadal grand challenge. <https://doi.org/10.53642/nrky9386>

Komyakova, V., Munday, P. L., & Jones, G. P. (2013). Relative Importance of Coral Cover, Habitat Complexity and Diversity in Determining the Structure of Reef Fish Communities. *PloS One*, 8(12), e83178–e83178. <https://doi.org/10.1371/journal.pone.0083178>

Leal, M. C., Ferrier-Pagès, C., Petersen, D., & Osinga, R. (2014). Coral aquaculture: Applying scientific knowledge to *ex situ* production. *Reviews in Aquaculture*, 8(2), 136–153. <https://doi.org/10.1111/raq.12087>

Lirman, D., & Schopmeyer, S. (2016). Ecological solutions to reef degradation: Optimizing coral reef restoration in the Caribbean and Western Atlantic. *PeerJ*, 4. <https://doi.org/10.7717/peerj.2597>

Madin, J.S., Hughes, T.P. and Connolly, S.R., 2012. Calcification, storm damage and population resilience of tabular corals under climate change. *PLoS ONE*, 7, p.e46637.

Munday, P.L., Jones, G.P., Pratchett, M.S. and Williams, A.J., 2008. Climate change and the future for coral reef fishes. *Fish and Fisheries*, 9(3), pp.261-285.

Muscatine, L., & Porter, J. W. (1977). Reef Corals: Mutualistic Symbioses Adapted to Nutrient-Poor Environments. *Bioscience*, 27(7), 454–460. <https://doi.org/10.2307/1297526>

National Academies of Sciences, Engineering, and Medicine (2019a). A Research Review of Interventions to Increase the Persistence and Resilience of Coral Reefs. Washington, DC: The National Academies Press. 246 pp.
<https://nap.nationalacademies.org/catalog/25279/a-research-review-of-interventions-to-increase-the-persistence-and-resilience-of-coral-reefs>

National Academies of Sciences, Engineering, and Medicine (2019b). A Decision Framework for Interventions to Increase the Persistence and Resilience of Coral Reefs. Washington, DC: The National Academies Press. 198 pp.
<https://nap.nationalacademies.org/catalog/25424/a-decision-framework-for-interventions-to-increase-the-persistence-and-resilience-of-coral-reefs>

Page, C. A., Muller, E. M., & Vaughan, D. E. (2018). Microfragmenting for the successful restoration of slow growing massive corals. *Ecological Engineering*, 123, 86–94.
<https://doi.org/10.1016/j.ecoleng.2018.08.017>

Pandolfi, J. M., Bradbury, R. H., Sala, E., Hughes, T. P., Bjorndal, K. A., Cooke, R. G., McArdle, D., McClenachan, L., Newman, M. J., Paredes, G., Warner, R. R., & Jackson, J. B. (2003). Global trajectories of the long-term decline of coral reef ecosystems. *Science*, 301(5635), 955–958. <https://doi.org/10.1126/science.1085706>

- Pandolfi, J.M., Connolly, S.R., Marshall, D.J. and Cohen, A.L., 2011. Projecting coral reef futures under global warming and ocean acidification. *science*, 333(6041), pp.418-422.
- Pörtner, H.O., Roberts, D.C., Adams, H., Adler, C., Aldunce, P., Ali, E., Begum, R.A., Betts, R., Kerr, R.B., Biesbroek, R. and Birkmann, J., 2022. Climate change 2022: Impacts, adaptation and vulnerability (p. 3056). Geneva, Switzerland:: IPCC.
- Rinkevich, B. (1995). Restoration Strategies for Coral Reefs Damaged by Recreational Activities: The Use of Sexual and Asexual Recruits. *Restoration Ecology*, 3(4), 241–251. <https://doi.org/10.1111/j.1526-100X.1995.tb00091.x>
- Soper, D. M., Villafranca, N., Dieffenthaler, J. P., Dieffenthaler, M., Tompkins, H., Weglarz, M., Vaughan, D., Hamlyn, S. B., & Stenesen, D. (2022). Growth and Cyclin-E Expression in the Stony Coral Species *Orbicella faveolata* Post-Microfragmentation. *The Biological Bulletin (Lancaster)*, 242(1), 40–47. <https://doi.org/10.1086/717926>
- Souter, D., Planes, S., Wicquart, J., Logan, M., Obura, D., Staub, F. (2021) Status of coral reefs of the world: 2020 report. Global Coral Reef Monitoring Network (GCRMN)/International Coral Reef Initiative (ICRI). <https://gcrmn.net/2020-report/>
- Setter, R.O., Franklin, E.C. and Mora, C., 2022. Co-occurring anthropogenic stressors reduce the timeframe of environmental viability for the world’s coral reefs. *PLoS biology*, 20(10), p.e3001821.
- Timmers, M. A., Jury, C. P., Vicente, J., Bahr, K. D., Webb, M. K., & Toonen, R. J. (2021). Biodiversity of coral reef cryptobiota shuffles but does not decline under the combined

- stressors of ocean warming and acidification. *Proceedings of the National Academy of Sciences*, 118(39). <https://doi.org/10.1073/pnas.2103275118>
- Tortolero-Langarica, J. J., Rodríguez-Troncoso, A. P., Cupul-Magaña, A. L., & Rinkevich, B. (2020). Micro-fragmentation as an effective and applied tool to restore remote reefs in the Eastern Tropical Pacific. *International Journal of Environmental Research and Public Health*, 17(18), 6574. <https://doi.org/10.3390/ijerph17186574>
- van Oppen M., Oliver, J., Putnam, H., and Gates, R.D. (2015). Building coral reef resilience through assisted evolution. *Proceedings of the National Academy of Sciences*. 112(8):2307-2313. <https://doi.org/10.1073/pnas.1422301112>
- Veron J.E.N., Stafford-Smith M.G., Turak E. and DeVantier L.M. (2016). Corals of the World. Accessed 12 Mar 2023, version 0.01. http://www.coralsoftheworld.org/species_factsheets/species_factsheet_summary/montipora-capitata/?version=0.01
- Wall, C. B., Ricci, C. A., Wen, A. D., Ledbetter, B. E., Klinger, D. E., Mydlarz, L. D., Gates, R. D., & Putnam, H. M. (2021). Shifting baselines: Physiological legacies contribute to the response of reef corals to frequent heatwaves. *Functional Ecology*, 35(6), 1366–1378. <https://doi.org/10.1111/1365-2435.13795>
- Young, C. N., Schopmeyer, S. A., & Lirman, D. (2012). A review of reef restoration and coral propagation using the threatened genus *acropora* in the Caribbean and Western Atlantic. *Bulletin of Marine Science*, 88(4), 1075–1098. <https://doi.org/10.5343/bms.2011.1143>

Zhao, X., Ma, X., Chen, B., Shang, Y., & Song, M. (2022). Challenges toward carbon neutrality in China: Strategies and countermeasures. *Resources, Conservation and Recycling*, 176, 105959. <https://doi.org/10.1016/j.resconrec.2021.105959>