Norwegian University
of Life Sciences

Master's Thesis 2019 60 ECTS
Faculty of Landscape and Society

Decadal Trends and Coral Acclimatization at Malauka‘a Fringing Reef, Kāne‘ohe Bay, O‘ahu, Hawai‘i

Kelsey Archer Barnhill
Tropical Ecology and Management of Natural Resources

kelseybarnhill@gmail.com

Noragric
Department of International Environment and Development Studies
The Faculty of Landscape and Society
P.O. Box 5003
N-1432 Ås
Norway
Tel.: +47 67 23 00 00
Internet: https://www.nmbu.no/fakultet/landsam/institutt/noragric

Declaration

I, Kelsey Archer Barnhill, declare that this thesis is a result of my research investigations and findings. Sources of information other than my own have been acknowledged and a reference list has been appended. This work has not been previously submitted to any other university for award of any type of academic degree.

Signature:

Kelsey A. Barnhill

Date: 01 May 2019

Table of Contents

Acknowledgements

I would like to express my gratitude to my co-supervisors Dr. Ian Bryceson and Dr. Keisha Bahr for their support throughout the entire thesis process. I am grateful for Dr. Bryceson's research advice over countless cups of tea and for his critiques of my drafts. I am so thankful for the tremendous support from Dr. Bahr from assisting in experimental design to providing statistical support and giving feedback on drafts of my thesis. I was encouraged every step of the way from my co-supervisors' academic expertise and enthusiasm for my thesis.

Special mention must go to Dr. Ku'ulei Rodgers who graciously hosted me at Hawai'i Institute of Marine Biology's Coral Reef Ecology Lab. I am indebted to her as well as to other members of the 'Point lab.' Thanks to Ashley McGowan, Yuko Stender, and Colleen Brown for their input and field assistance.

I also must thank Dr. Annette Breckwoldt, who conducted the original 2000 surveys and managed to provide me with the raw data from 18 years ago.

Thank you to Snorre Sundsbø and Huynh Bao Ngan for assisting me with statistical analyses in R studio.

Following a field-work hiccup, I would not have been able to finish my reef surveys without the help of Ilina Gobburu, Leah Shizuru, Ashley Fossett, Lilly Thomey, and my father, Robert 'Barney' Barnhill who all laid out transects, took photographs, and managed equipment for me.

I am dedicating this thesis to my parents, Barney Barnhill and Cindy Archer, who have always supported my endeavors- no matter where in the world they take me.

Abstract

Globally, coral reefs are under threat from climate change and increasingly frequent bleaching events. However, corals in Kāneʻohe Bay have repeatedly shown resilience and the ability to acclimatize to rising temperatures and increased frequencies of bleaching events. The Malaukaʻa fringing reef -first surveyed in 2000- is revisited to compare species composition and percent cover of corals, algae, and mixed sand to investigate how the reef has fared over 18 years. Despite climate change-induced temperature increases and two major bleaching events, the fringing reef saw no significant change in total coral cover percent, nor a change in percent cover of the two dominant reef-building corals: *Montipora capitata* and *Porites compressa*. However, the loss of two coral species and addition of one new coral species between surveys indicates that while the fringing reef remains intact, a shift in species composition has occurred. While locally rare species from the 2000 study were not found in 2018, the reef remains. The survival of the fringing reef studied indicates resilience and suggests these Hawaiian corals are capable of acclimatization to climate change and bleaching events. A reciprocal transplant experiment was also conducted to determine if calcification (linear extension and accretion) for *M. capitata* and *P. compressa* varied between two sites 600 meters apart at either end of the surveyed reef and whether or not genetics or environmental factors were responsible for the differences. Linear extension did not vary between sites for either species, however accretion (measured as change in mg g^{-1} d^{-1}) was significantly different between sites for *P. compressa*. Differences in accretion following transplantation suggest both environment and genetics impacted calcification of *P. compressa* in Kāneʻohe Bay.

Synthesis

Coral reefs are one of the most biodiverse ecosystems in the world, providing ecosystem goods and services such as fisheries, cultural benefits, and coastal protection (Moberg & Folke, 1999). However, reef ecosystems around the globe are in anthropogenically-driven ecological declines which can lead to a phase shift from coral-dominated reefs to algae-dominated reefs (De'ath et al., 2012; Bonaldo & Hay, 2014). Climate change-driven increasing sea surface temperatures threaten coral reefs globally as thermal stress can cause coral bleaching (Hoegh-Guldberg et al. 2007; Jokiel & Coles, 1990). Some Hawaiian corals, however, have shown resilience through acclimatizing to thermal stress and resisting coral bleaching (Coles et al., 2018). Reefs in Hawaii have proven to be more resilient than reefs in other regions as they have sustained their percent coral cover from 1999-2012 while other reefs were in decline (Rodgers et al., 2015; De'ath et al., 2012).

Corals in Kāneʻohe Bay, O'ahu (one of the most intensively studied estuarine-reef systems in the world) have repeatedly demonstrated their resilience to anthropogenic and environmental stressors such as bleaching events (Bahr et al., 2017). Kāneʻohe Bay is an excellent site to study coral resilience as the bay represents one of the few examples of a phase shift reversal back to coral after an algae-dominated phase (Stimson, 2018). Coral reefs have persisted in the bay following dredging, years of effluent sewage output, flood-induced freshwater kills, and three major thermal-induced bleaching events (Reviewed in Bahr et al., 2015). In spite of major environmental stressors, Kāneʻohe Bay retains one of the highest levels of coral cover across the Hawaiian islands (Jokiel et al., 1993; Rodgers et al., 2015).

A masters thesis from nearly 2 decades ago (Mühlig-Hofmann, 2001) surveyed a 600 meter section of Kāneʻohe Bay's Malauka`a fringing reef which had yet to be repeated. The paper for the first chapter of this thesis: *Decadal Trends and Coral Resilience at Malauka`a Fringing Reef, Kāneʻohe Bay, O'ahu* returns to Malauka`a fringing reef to explore how the reef has fared in the 18 years since its initial survey. Has the reef shown resilience through maintaining coral cover and biodiversity at levels similar to the 2000 survey, despite facing climate change induced sea surface temperature increases and two major bleaching events over the 18 years?

Following the resurvey of Malauka`a fringing reef, differences in benthic cover in the North and South portions of the reef drove the paper for the second chapter of this thesis: *Reciprocal Transplant Demonstrates Acclimatization in Porites compressa and Montipora capitata, Kāneʻohe Bay, O'ahu*. Through a reciprocal transplant experiment, environmental and genetic influences on calcification at the two ends of the reef are explored.

These two papers converge on the theme of reef resilience to global (i.e. thermal stress from climate change) and local (e.g. depressed aragonite saturation levels, low salinity levels, etc.) stressors as corals at the Malauka`a fringing reef endure.

Reference List

Bahr, K. D., Jokiel, P. L., & Toonen, R. J. (2015). The unnatural history of Kāne ʻohe Bay: coral reef resilience in the face of centuries of anthropogenic impacts. *PeerJ*, *3*, e950.

Bahr, K. D., Rodgers, K. U. S., & Jokiel, P. L. (2017). Impact of Three Bleaching Events on the Reef Resiliency of Kāne ʻohe Bay, Hawai ʻi. *Frontiers in Marine Science*, *4*, 398.

Bonaldo, R. M., & Hay, M. E. (2014). Seaweed-coral interactions: variance in seaweed allelopathy, coral susceptibility, and potential effects on coral resilience. *PloS one*, *9*(1), e85786.

Coles, S. L., Bahr, K. D., Ku'ulei, S. R., May, S. L., McGowan, A. E., Tsang, A., ... & Han, J. H. (2018). Evidence of acclimatization or adaptation in Hawaiian corals to higher ocean temperatures. *PeerJ*, *6*, e5347.

De'ath, 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.

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., ... & Knowlton, N. (2007). Coral reefs under rapid climate change and ocean acidification. *Science*, *318*(5857), 1737-1742.

Jokiel, P. L., & Coles, S. L. (1990). Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. *Coral reefs*, *8*(4), 155-162.

Jokiel, P. L., Hunter, C. L., Taguchi, S., & Watarai, L. (1993). Ecological impact of a fresh-water "reef kill" in Kaneohe Bay, Oahu, Hawaii. *Coral Reefs*, *12*(3-4), 177-184.

Moberg, F., & Folke, C. (1999). Ecological goods and services of coral reef ecosystems. *Ecological economics*, *29*(2), 215-233.

Mühlig-Hofmann, A. (2001). *The distribution of corals and macroalgae in relation to freshwater and sediment discharge on a fringing reef in Kane'ohe Bay, O'ahu, Hawai'i* (Masters thesis). University of Bremen, Germany.

Rodgers, K. U. S., Jokiel, P. L., Brown, E. K., Hau, S., & Sparks, R. (2015). Over a decade of change in spatial and temporal dynamics of Hawaiian coral reef communities. *Pacific Science*, *69*(1), 1-13.

Stimson, J. (2018). Recovery of coral cover in records spanning 44 yr for reefs in Kāneʻohe Bay, Oaʻhu, Hawai ʻi. *Coral Reefs*, *37*(1), 55-69.

Chapter 1

Decadal Trends and Coral Resilience at Malauka`a Fringing Reef, Kāne‘ohe Bay, O’ahu

Kelsey A. Barnhill[1], Keisha D. Bahr[2]

[1]Faculty of Environmental Sciences and Natural Resources, Norwegian University of Life Sciences

[2]Department of Life Sciences, Texas A&M University-Corpus Christi

Abstract

Globally, coral reefs are under threat from climate change and increasingly frequent bleaching events. Yet, corals in Kāne‘ohe Bay have demonstrated the ability to acclimatize and resist increasing temperatures. The Malauka`a fringing reef, first surveyed in 2000, is revisited to compare species composition and percent cover of corals, algae, and mixed sand to investigate how the reef has fared over 18 years. Despite climate change induced temperature increases and two major bleaching events, the fringing reef saw no significant change in total coral cover percent, nor a change in percent cover of the two dominant reef-building corals: *Porites compressa* and *Montipora capitata*. However, the loss of two coral species and addition of one new coral species between surveys indicates that while the fringing reef remains intact, a shift in species composition has occurred. While locally rare species from the 2000 study were not found in 2018, the reef itself remains. The survival of the fringing reef studied indicates resilience and suggests these Hawaiian corals are capable of acclimatization to climate change and bleaching events.

Keywords: coral reefs, macroalgae, resilience, species composition

Introduction

Warming sea surface temperatures caused by climate change threaten coral reefs globally (Hoegh-Guldberg et al. 2007). Increased water temperatures cause coral bleaching (reviewed in Jokiel & Coles, 1990) which can cause total or partial mortality for colonies if the corals are unable to recover (reviewed in Baker et al., 2008). Coral mortality leads to reef degradation as the reef loses structural complexity and is overgrown by algae, often leading to an algae-dominated phase shift (Graham et al., 2006). Reef degradation directly causes the loss of reef-related ecosystem services such as seafood production, shoreline protection, habitat provision, materials for medicines, and nitrogen fixation, among others (Moberg & Folke, 1999).

Significant ecological declines driven by anthropogenic stressors are occurring on coral reefs around the world (De’ath et al., 2012). In 2000 an estimated 11% of all coral reefs had already been lost with an additional 16% damaged beyond the point of being functional ecosystems

(Wilkinson, 2000). From 1985-2012 the Great Barrier Reef experienced a 50.7% decrease in coral cover (De'ath et al., 2012) and coral cover in the entire Indo-Pacific is 20% less than historical levels from 100 years ago (Bruno & Selig, 2007). Hawaiian reefs, however, have one of the lowest threat ratings in the Pacific (less than 30% threatened) (Burke et al., 2011). From 1999-2012 mean Hawaiian coral cover and diversity remained stable statewide, including within Kāneʻohe Bay (Rodgers et al., 2015). Reefs within Kāneʻohe Bay have repeatedly shown resilience by recovering from natural and anthropogenic disturbances such as bleaching events (Bahr et al., 2017). Increasingly frequent bleaching events threaten the longevity of coral reef ecosystems (Hughes et al., 2017) and whether or not corals can become adaptive or resistant to bleaching is contested in current literature (Hughes et al., 2017). However, corals in Kāneʻohe Bay have shown resilience through acclimatization to increased temperatures (Coles et al., 2018).

Kāneʻohe Bay

Kāneʻohe Bay is located on the northeast side of Oʻahu, Hawaiʻi (21°4ʻ N and 157°8' W). The bay has some of the highest levels of coral cover (54-68% compared to statewide average of 24.1%) across the Hawaiian islands (Bahr et al., 2017; Jokiel et al., 1993; Rodgers et al., 2015). Reefs in the bay experience elevated temperatures which offshore reefs will not be subjected to for several years due to restricted circulation which increases summer water temperatures by 1-2° Celsius (Bahr et al., 2015b).

Kāneʻohe Bay represents one of the few recorded examples of a phase shift back to coral following an extended algae-dominated phase (Stimson, 2018). From 1960-1970 the population in Kāneʻohe doubled leading to effluent municipal and military sewage to be discharged in the bay, causing eutrophication and a subsequent decline in coral cover and diversity (Banner, 1974). Following the release of effluent sewage into the bay, the algae *Dictyosphaeria cavernosa,* stimulated by increased nutrient availability, spread widely, causing a phase shift from coral-dominated to algae-dominated (Smith et al., 1981; Stimson et al., 2001). Following the 1979 sewage diversion, coral cover in the bay more than doubled in just four years (Hunter & Evans, 1995) as nutrient levels decreased (Smith et al., 1981).

Experiencing the effects of climate change for the first time, corals across Kāneʻohe Bay first bleached in 1996 but recovered within months causing only 2% total mortality (Jokiel & Brown, 2004). A second, more severe bleaching event occurred in 2014 (Bahr et al., 2015b). While nearly half of all corals in the southern region of the bay were pale or bleached immediately following the 2014 bleaching, there was only 1% total coral mortality 3 months later (Bahr et al., 2015a). In 2015 another widespread bleaching event affected the Kāneʻohe Bay reefs, however a 15% decrease in bleaching compared to the 2014 event suggested some corals may be acclimatizing to increased temperatures (Bahr et al., 2017). Kāneʻohe Bay has retained high coral cover despite Hawaiian offshore water temperatures increasing by 1.15° Celsius over the past 60 years (Bahr et al., 2017). The historical resilience of corals in Kāneʻohe Bay and the consistently high coral cover while many reefs around the globe are in decline led to the research question: How has species percent cover and community composition changed in response to 18 years of warming temperatures and 2 major bleaching events at Malauka`a fringing reef?

Methods

Study Site

The study site was a 600-meter section of the Malauka`a fringing reef (21.44300899°N, -157.80636°W to 21.43853104°N, -157.806541°W) in the south-west of Kāneʻohe Bay which was initially surveyed in 2000 (Mühlig-Hofmann, 2001). Similar to other reefs in the bay, *Porites compressa* and *Montipora capitata* are the dominant reef-building corals. The northern section of the reef is approximately 125 meters offshore of Kealohi Point at He'eia State park. The southern 200 meters of the study site is adjacent to the Paepae o Heʻeia (traditional Hawaiian fishpond) where there is ongoing estuarine restoration focusing on socio-cultural benefits (Bremer et al., 2018). The southern end of the reef is subjected to freshwater stream and pond output from He'eia stream and a triple mākāhā (sluice gate) within Paepae o Heʻeia (Möhlenkamp, 2019).

Experimental setup

Benthic Survey

A modified version of the Point Intercept Transect (PIT) as described by Hill & Wilkinson (2004) was used in both the 2000 and 2018 surveys. The PIT method identifies benthic cover every 50 centimeters along a transect (Jokiel, et al. 2015). During the 2000 study (Mühlig-Hofmann, 2001) benthic cover was recorded every meter and thus repeated as such in the 2018 study. Additionally, transects from the 2000 study continued until the edge of the reef platform was reached, causing transects to consist of varying lengths dependent on the width of the reef. A Garmin GPSMAP 78s was used to mark the 60 transects which were spaced 10 meters apart to survey the 600 meter portion of the fringing reef (Figure 1). The locations of the 2000 transects were replicated in 2018 to the best of our ability. Both surveys were conducted with one snorkeling observer identifying all species *in situ*.

Figure 1. Map of Malauka`a fringing reef with transects overlaid within Kāneʻohe Bay, O'ahu. Note the variation in transect length due to reef width. Photo Credit: Digital Globe.

Temperature

Temperatures were recorded at various sites along the fringing reef for one month from mid-September 2000 to mid-October in 2000 at depths of 35-40 cm (YSI Inc. Model 30/10 FT). Hobo Water Temp Pro temperature loggers (Onset Computer Corporation) continuously recorded temperatures at 30 minute intervals at 9 of the sites from the 2000 survey from mid-September 2017 to mid-October 2017 to compare temperature changes between years (McGowan, unpublished data). Temperature data is from 2017 as opposed to 2018 as the benthic survey took place in July 2018. Time of temperature recordings was not noted in the 2000 data whereas 12:00 noon was selected for 2017 temperatures.

Statistical Analysis

A Permutational multivariate analysis of variances (PERMANOVA) was used to determine if overall species composition changed between 2000 and 2018 within R studio (RStudio Team, 2015). A Non-metric multidimensional scaling (NMDS) ordination plot was created to visualize the 2000 and 2018 benthic communities within R studio (RStudio Team, 2015). A Matched Pair analysis was used to compare changes in temperatures between years (2000 vs 2017) within sites as well as individual species and groups (i.e. corals, algae, and sand/sediments) between years (2000 vs 2018) within transects using JMP 13 Pro (SAS Institute Inc., USA).

Results

Benthic Survey

Transects ranged from 6 to 32 meters in length, with 1219 observations recorded at one meter intervals along the fringing reef in both 2000 and 2018. Six species of coral (i.e., *Porites compressa, Porites lobata, Montipora capitata, Lobactis* (formally *Fungia*) *scutaria, Pocillopora damicornis, Pocillopora meandrina*) were recorded at the site in 2000 and four (i.e., *P. compressa, M. capitata, P. damicornis, Leptastrea purpurea*) were recorded in 2018. Four species of macroalgae (i.e. *Dictyosphaeria cavernosa*, *Dictyosphaeria versluyii*, *Gracilaria salicornia, Kappaphycus alvarezii*) were present in 2000 and two (i.e. *D. cavernosa*, *D. versluyii*) in 2018. Unidentified species of turf algae, crustose coralline algae, and mixed sand and rubble were present in both surveys.

Statistical Analysis

Temperature

The mean temperature at the site increased from 27.50 ± 1.13° Celsius in 2000 to 28.68 ± 0.43° Celsius in 2017 ($p < 0.0001$).

Community-level changes

Overall community composition at the site changed from 2000 to 2018 (F model= 17.47, $p = 0.001$, PERMANOVA) (Figure 2).

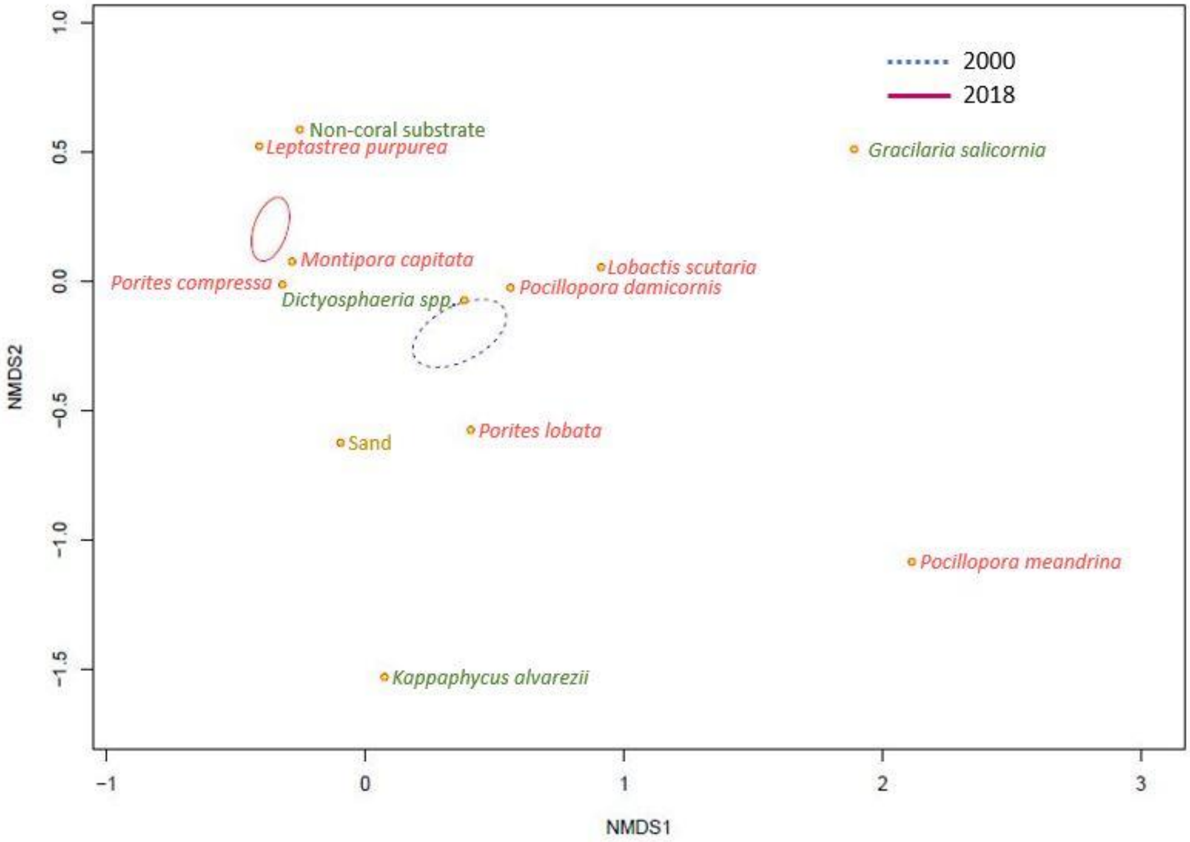


Figure 2. Non-metric multidimensional scaling (NMDS) ordination plot representing the benthic communities from the 2000 and 2018 surveys (Dimensions = 2, Stress < 0.2). Ellipses represent 95% confidence intervals of each community. Coral species are written in pink, algae in green, and sand in yellow.

Mixed Sand and Rubble

Total mixed sand and rubble cover decreased significantly from 12% to 4.6% from 2000 to 2018 ($p < 0.0001$) (Figure 3, Figure 4).

Algae

The total overall algae cover increased significantly from 42.9% in 2000 to 56.8% in 2018 ($p = 0.001$) (Figure 3, Figure 4). *Dictyosphaeria spp.* (*D. cavernosa* and *D. versluyii*) decreased significantly from 16.7% in 2000 to 1.1% 2018 ($p < 0.0001$). *Gracilaria salicornia* and *Kappaphycus alvarezii* were both present in 2000 (2.8%, and 0.33% respectively) and absent from the 2018 survey ($p = 0.0008, 0.045$). Non-coral substrate (turf, crustose coralline algae) increased significantly from 23.1% in 2000 to 55.6% in 2018 ($p < 0.0001$).

Corals

The change in total overall coral cover was insignificant with 45.1% in 2000 and 38.6% in 2018 (p = 0.0637) (Figure 3, Figure 4). Neither dominant reef-building species *Porites compressa* nor *Montipora capitata* experienced a significant change in percent cover as *P. compressa* was found to cover 33.6% and 33.7% of the reef (p = 0.9618) and *M. capitata* 4.4% and 4.2% (p = 0.8207) in 2000 and 2018, respectively. *Porites lobata* (5%, p < 0.0001), *Pocillopora meandrina* (0.16%, p = 0.1590), and *Lobactis scutaria* (0.16%, p = 0.1590) were all present in the 2000 survey but absent in 2018 (however, *L. scutaria* was observed on the reef but did not land on any survey marks). *Pocillopora damicornis* decreased significantly from 1.8% to 0.25% from 2000 to 2018 (p = 0.0006). *Leptastrea purpurea* was not present in the 2000 survey but represented 0.49% total cover in 2018 (p = 0.0327).

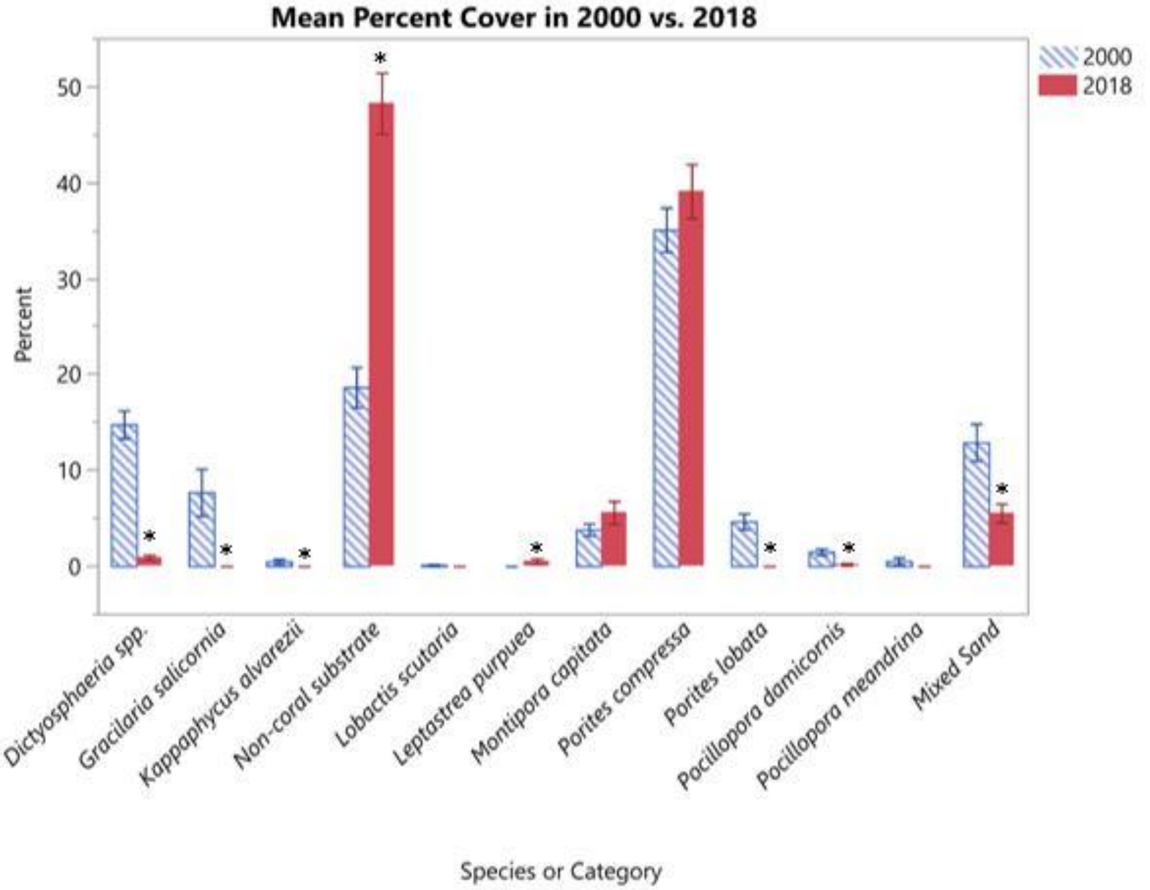


Figure 3. Mean Percent cover of each species or category in 2000 vs. 2018. Each standard error bar is one standard error from the mean. * Indicates significant difference between years at p < 0.05

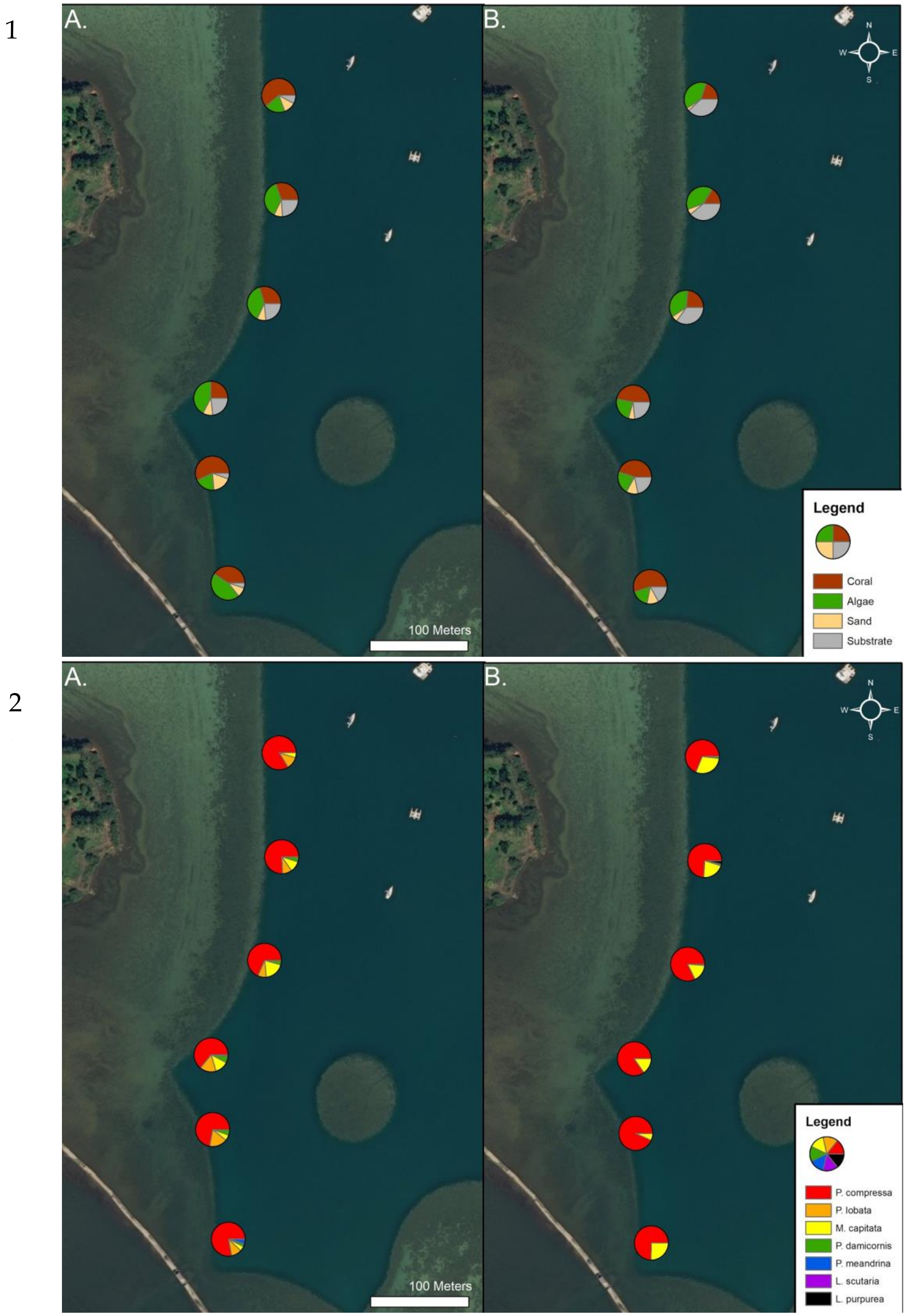


Figure 4. Spatial trends in 1) Total benthic cover and 2) coral species composition. A. 2000 survey, B. 2018 survey. Photo credit: Digital Globe

Discussion

While many reefs globally are in decline due to anthropogenic factors, Hawaiian coral cover has remained stable from 1999-2012 (Rodgers et al., 2015). Returning to the Malauka`a fringing reef provided an opportunity to explore decadal trends in coral cover across an entire 600-meter reef. This study explores how Malauka`a fringing reef has fared over the past 18 years, comparing the site to reefs across the Hawaiian islands. We predict the reef will show the same resilience as other Hawaiian reefs through maintaining high coral cover in the face of climate change like most Kāneʻohe Bay reefs.

Temperature

Temperature increased by more than 1° Celsius along the fringing reef from 2000 to 2017. However, the time of day which the temperature was taken in 2000 was not specified, and the large variation (SD = 1.13 in 2000 compared to 0.43 in 2017) suggests temperatures may not have been taken at the same time each day. Therefore, while the data points to increasing temperatures, the uncertainty in the 2000 data makes the comparison unreliable. As Hawaiian offshore water temperatures have risen by 1.15° Celsius over the past 60 years (Bahr et al., 2017), the observed 1.18° increase in 17 years at the study site is likely influenced by error possibly caused by deviation in temperature recording times between years.

Mixed Sand and Rubble

The significant decrease in percent cover of mixed sand and rubble indicates the reef expanded between surveys. This is further supported by a break in the fringing reef in 2000 (represented as a transect with 100% sand cover) which was not observed in the 2018 survey.

Algae

Dictyosphaeria cavernosa was once the dominant algae species in Kāneʻohe Bay, responsible for one of the first well-studied reef phase shifts from coral-dominated to algae dominated (Stimson et al., 2001). The release of effluent sewage in the 1970's provided particulate nutrients to stimulate growth of *D. cavernosa*, causing the phase shift (Smith et al., 1981). Following sewage diversion, the algae persisted in the bay due to overfishing of herbivorous fish that would have placed grazing pressure on the species (Stimson et al., 2001). *D. cavernosa* remained abundant in Kāneʻohe Bay, averaging 16% total cover during a 1996-1997 survey (Stimson et al., 2001). The findings of the 2000 survey indicate the percent cover of *Dictyosphaeria spp.* remained at a comparable level 3 years later at the fringing reef (16.7%). In 2006, following an unusually rainy period, decreased irradiance combined with slow spring growth rates for the species caused *D. cavernosa* to effectively disappear from the bay (Stimson & Conklin, 2008). Immediately following the rapid decline, reefs nearby Moku o Loe averaged 0-4% total cover of *D. cavernosa*

(Stimson & Conklin, 2008). Twelve years later, the prevalence of *D. cavernosa* has remained greatly diminished at this fringing reef (1.1%), suggesting an enduring phase shift reversal.

The invasive species *G. salicornia* was introduced to Kāneʻohe Bay in the 1970's and quickly spread, overgrowing and smothering reef-building corals (Smith et al., 2004). The invasive algae has since decreased over the past few years as a result of biocontrol (Stimson et al., 2007), manual removal (Neilson, et al., 2018), and increased grazing from *Chelonia mydas,* a green sea turtle (Bahr, et al., 2018). The management efforts and return of *C. mydas* to Kāneʻohe Bay likely explain why the once dominant macroalgae was not observed during the 2018 survey.

Like *G. salicornia*, *Kappaphycus alvarezii* (formerly *Eucheuma striatum*) was introduced to Kāneʻohe Bay in the 1970's (Russel, 1983) and had spread across the southern and central bay by 1996 in a near-cosmopolitan distribution (Rodgers & Cox, 1999). A total percent cover of 0.33% in the 2000 survey was slightly higher than the mean 0.06 ± 0.02% cover found at four shallow fringing reefs in the central bay in 1996 (Rodgers & Cox, 1999). Amidst fears of further spreading, preliminary management options for *Kappaphycus spp.* were assessed in 2002 (Conklin & Smith, 2005). Divers used an underwater vacuum and outplanted juvenile urchins (*Tripneustes gratilla*) to remove and control the species in 2011-2013, leading to an 85% decrease in invasive macroalgae across sites (Neilson et al., 2018). Management efforts have continued to be successful as *K. alvarezii* was not observed at the study site during the 2018 survey.

Despite *Dictyosphaeria spp., G. salicornia,* and *K. alvarezii* all decreasing or disappearing from the reef, a total increase in algae percent cover from 2000 to 2018 was observed, mainly due to the increase in 'non-coral substrate'. It should be noted that 18.6% of the non-coral substrate from the 2018 survey was crustose coralline algae (CCA). CCA was not given its own category as CCA was not differentiated from 'encrusted corals' in the 2000 study. Thus, the percent cover of total algae as well as non-coral substrate is inflated in the 2018 data and likely the 2000 data as well. Unlike turf and macroalgae, CCA promotes coral recruitment and recovery (Price, 2010) and would have ideally been separated into its own category. The high percentage of non-coral substrate in 2018 (55.6%) was also impacted by the prevalence of (perhaps short-lived) turf on the tips of *P. compressa* and *M. capitata.* The tips of these reef-building corals were susceptible to warming events and air exposure at extreme low tides as the 2018 survey was conducted in late July following a warm period and spring tides (Figure 5). Most algae observed in the 2018 survey was found on the Northern portion of the reef (Figure 4).

Figure 5. Reef exposed during low tide in Kāne‘ohe Bay (Picture Credit: Dr. Keisha Bahr). Tips of a pale *P. compressa* colony covered with turf (Picture Credit: Kelsey Barnhill).

Corals

Despite a significant increase in algae percent cover between surveys, total coral percent cover was similar in 2000 and 2018.

Porites compressa sustained a high percent cover over 18 years at the fringing reef despite decreasing in percent cover by 22.9% in 14 years (1999-2012) across the Hawaiian islands, with significant declines on the island of O’ahu (Rodgers et al., 2015). *Porites compressa* is known to be sensitive to increased temperatures which can cause bleaching and decreased calcification rates for the species (Carricart-Ganivet et al., 2012). Despite temperature increases over the 18 years, *P. compressa* has maintained its dominance as the most prevalent coral species at Malauka`a fringing reef, implying the ability to acclimatize and persist in warming waters.

Montipora capitata percent cover remained at a similar level between surveys despite increasing in percent cover by 56.8% in 14 years (1999-2012) across the Hawaiian islands (Rodgers et al., 2015). However, this study extended transects only to the end of the continuous reef pavement and many *M. capitata* colonies were located inshore of the reef (personal observation). *Montipora capitata* colonies in Kāne‘ohe Bay have shown resilience through the ability to acclimatize/adapt to temperature increases in lab experiments (Coles et al., 2018). The continued presence of *M. capitata* at Malauka`a fringing reef despite temperature increases supports the findings of Coles et al. (2018) through indicating resilience not just in lab manipulations, but in the field as well.

Percent cover of *Pocillopora damicornis* decreased significantly between the 18 years. The species is known to be highly sensitive to decreased salinity levels (Jokiel et al., 1993). Increased freshwater input onto the southern portion of the surveyed reef may have impacted the abundance of *P. damicornis*. Following biocultural restoration of the Paepae o He‘eia, water exchange between the fishpond and the adjacent reef increased, with an additional 14,418 m^3 of pond water being flushed out onto the reef during each ebb tidal cycle (Möhlenkamp, 2019)

In 2000, *P. lobata* was a common reef-building coral at the study site. However, *P. lobata* was not observed in the 2018 survey. *P. lobata* was described as ‘common to Kāne‘ohe Bay’ in 1999 (Grottoli, 1999), however more recently it was estimated to have 0-1% cover along Kāne‘ohe’s fringing reefs (Franklin et al., 2013). There is now evidence *P. lobata* and *P. compressa* may be different morphotypes of the same species or hybridize frequently (Forsman et al., 2017). If this is the case, the disappearance of *P. lobata* may mean one morphospecies is selected over the other and there has not been a decrease in biodiversity for *Porites*. Due to similarities between *P. lobata* and *P. compressa* as well as the possibility of hybridizations, there may have been misidentifications in the 2000 survey.

Similar to *P. lobata*, *P. meandrina* was also estimated to have 0-1% cover along fringing reefs in Kāne‘ohe Bay, supporting its absence in the 2018 survey (Franklin et al., 2013). *Pocillopora meandrina* has been similarly decreasing in percent cover across the Hawaiian islands, with a 36.1% decrease from 1999-2012 (Rodgers et al., 2015). Following the 2015 bleaching event, 98% of *P. meandrina* colonies on the west side of the island of Hawai’i were partially or fully bleached, demonstrating they are one of the more susceptible species to thermal stress (Maynard et al., 2016). They were similarly listed as the least resistant species to thermal stress at Kahe Point, O’ahu (Jokiel & Coles, 1974). The species vulnerability to increased temperatures may explain its disappearance in the 2018 survey.

Lobactis scutaria was recorded during the 2000 survey but not observed in the 2018 survey. While it did not appear in the survey, it is present at the study site (personal observation). While present, the absence from the survey would classify *L. scutaria* as ‘very rare’ (Jokiel & Maragos, 1978). Low densities of *L. scutaria* are expected at the site, as the species is abundantly found on patch reefs in Kāne‘ohe Bay, not fringing reefs (Lacks, 2000). Future studies of the area should employee a survey method such as the ‘quadrat method’ which avoids sampling from a small number of points to ensure rare and very rare species are included (Jokiel, et al., 2015).

Leptastrea purpurea was the only new species seen in the 2018 survey. This encrusting species is tolerant to elevated temperatures and has been seen in areas where other coral species have succumbed to thermal stress (Jokiel & Coles, 1974). The hardy species has been declared one of the ‘long-term winners’ as *L. purpurea* increase in abundance during thermal stress events (van

Woesik et al., 2011). *Leptastrea purpurea* has a relatively low metabolic rate, a characteristic known to help corals tolerate high temperatures (Mayer, 1917). Increasing temperatures may have allowed *L. purpurea* to settle in an area it had not before been present in, as it now holds a competitive advantage over other species which are less tolerant to thermal stress.

Coral cover did not change significantly over the past 18 years although two bleaching events (2014 and 2015) occurred during that time frame. While the fringing reef has shown resilience, it is unclear whether or not acclimatization and resistance to climate change has impacted its success. Coles et al. (2018) found all three species (i.e., *M. capitata, L. scutaria, P. damicornis*) of Hawaiian corals tested within Kāneʻohe Bay have higher survivorship at 31°C today than they did in 1970 suggesting these corals can adapt to higher temperatures. As the corals in this study were from similar locations as those used by Coles et al. (2018), it is possible the resilience seen on the reef can be attributed in part to adaptation or acclimatization.

While the total coral cover remained relatively stable over the past 18 years, the species composition changed. The decrease in the total number of coral species present in the survey (6 in 2000, 4 in 2018) represents an overall loss in biodiversity. Additionally, two (or one if *P. lobata* is considered to be the same species as *P. compressa*) species of coral were lost in the 18 years while one non-reef building coral (*L. purpurea*) was added. This change suggests a temperature-driven shift in species composition over the 18 years. Even though the total coral cover remains high, the loss of locally uncommon species has negative impacts as rarer species often support more vulnerable and unique ecosystem functions (Mouillot, 2013).

Despite a shift in coral biodiversity, total coral cover percent remained unchanged over the 18 years and populations of the two dominant species of coral remained at comparable levels. Despite evidence of Hawaiian coral adaptation to increased temperatures, this adaptation might not occur fast enough to tolerate projected increasingly frequent bleaching events (Coles et al., 2018). While the Malauka`a fringing reef has shown resilience over the past 18 years, its future is uncertain.

Author Contributions

Kelsey A. Barnhill conceived and designed the project, collected the data, analyzed the data, prepared figures and/or tables, and authored drafts of the paper
Keisha D. Bahr conceived and designed the project, prepared figures and/or tables, and reviewed/edited drafts of the paper.

Reference List

Bahr, K. D., Coffey, D. M., Rodgers, K. & Balazs, G. H. (2018). Observations of a rapid decline in invasive macroalgal cover linked to green turtle grazing in a Hawaiian marine reserve. *Micronesica* 2018- 07, 11 pp.

Bahr, K. D., Jokiel, P. L., & Rodgers, K. S. (2015a). The 2014 coral bleaching and freshwater flood events in Kāneʻohe Bay, Hawaiʻi. *PeerJ, 3,* e1136.

Bahr, K. D., Jokiel, P. L., & Toonen, R. J. (2015b). The unnatural history of Kāne ʻohe Bay: coral reef resilience in the face of centuries of anthropogenic impacts. *PeerJ*, *3*, e950.

Bahr, K. D., Rodgers, K. U. S., & Jokiel, P. L. (2017). Impact of Three Bleaching Events on the Reef Resiliency of Kāne ʻohe Bay, Hawai ʻi. *Frontiers in Marine Science*, *4*, 398.

Baker, A. C., Glynn, P. W., & Riegl, B. (2008). Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuarine, coastal and shelf science*, *80*(4), 435-471.

Banner, A. H. (1974). Kaneohe Bay, Hawaii; Urban pollution and a coral reefs ecosystem. In Proc. 2nd. Int. Coral Reef Symp. (Vol. 2, pp. 685-70).

Bremer, L., Falinski, K., Ching, C., Wada, C., Burnett, K., Kukea-Shultz, K., ... & Ticktin, T. (2018). Biocultural Restoration of Traditional Agriculture: Cultural, Environmental, and Economic Outcomes of Lo ʻi Kalo Restoration in Heʻeia, O ʻahu. *Sustainability*, *10*(12), 4502.

Bruno, J. F., & Selig, E. R. (2007). Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS one*, *2*(8), e711.

Burke, L., Reytar, K., Spalding, M., & Perry, A. (2011). Reefs at risk. *World Resources Institute, Washington, DC, 124*.

Carricart-Ganivet, J. P., Cabanillas-Teran, N., Cruz-Ortega, I., & Blanchon, P. (2012). Sensitivity of calcification to thermal stress varies among genera of massive reef-building corals. *PLoS One*, *7*(3), e32859.

Coles, S. L., Bahr, K. D., Ku'ulei, S. R., May, S. L., McGowan, A. E., Tsang, A., ... & Han, J. H. (2018). Evidence of acclimatization or adaptation in Hawaiian corals to higher ocean temperatures. *PeerJ*, *6*, e5347.

Conklin, E. J., & Smith, J. E. (2005). Abundance and spread of the invasive red algae, Kappaphycus spp., in Kane'ohe Bay, Hawai'i and an experimental assessment of management options. *Biological Invasions*, *7*(6), 1029-1039.

De'ath, 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.

Forsman, Z. H., Knapp, I. S. S., Tisthammer, K., Eaton, D. A. R., Belcaid, M., & Toonen, R. J. (2017). Coral hybridization or phenotypic variation? Genomic data reveal gene flow between Porites lobata and P. Compressa. *Molecular phylogenetics and evolution*, *111*, 132-148.

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.

Franklin E. C., Jokiel P. L., Donahue M. J. (2013). Data from: Predictive modeling of coral distribution and abundance in the Hawaiian Islands. *Dryad Digital Repository.* http://dx.doi.org/10.5061/dryad.9vd0q

Graham, N. A., Wilson, S. K., Jennings, S., Polunin, N. V., Bijoux, J. P., & Robinson, J. (2006). Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences*, *103*(22), 8425-8429.

Grottoli, A. G. (1999). Variability of stable isotopes and maximum linear extension in reef-coral skeletons at Kaneohe Bay, Hawaii. *Marine Biology*, *135*(3), 437-449.

Hill, J. & Wilkinson, C. (2004). Methods for ecological monitoring of coral reefs. *Australian Institute of Marine Science*, Townsville, 117.

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., ... & Knowlton, N. (2007). Coral reefs under rapid climate change and ocean acidification. *Science, 318*(5857), 1737-1742.

Hughes, T. P., Kerry, J. T., Álvarez-Noriega, M., Álvarez-Romero, J. G., Anderson, K. D., Baird, A. H., ... & Bridge, T. C. (2017). Global warming and recurrent mass bleaching of corals. *Nature, 543*(7645), 373.

Hunter, C. L., & Evans, C. W. (1995). Coral reefs in Kaneohe Bay, Hawaii: two centuries of western influence and two decades of data. *Bulletin of Marine Science*, *57*(2), 501-515.

JMP®, Version *13 Pro*. SAS Institute Inc.,Cary, NC, 1989-2019.

Jokiel, P. L., & Brown, E. K. (2004). Global warming, regional trends and inshore environmental conditions influence coral bleaching in Hawaii. *Global Change Biology*, *10*(10), 1627-1641.

Jokiel, P. L., & Coles, S. L. (1974). Effects of heated effluent on hermatypic corals at Kahe Point, Oahu. *Pacific Science, 28.*

Jokiel, P. L., & Coles, S. L. (1990). Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. *Coral reefs*, *8*(4), 155-162.

Jokiel, P. L., Hunter, C. L., Taguchi, S., & Watarai, L. (1993). Ecological impact of a fresh-water "reef kill" in Kaneohe Bay, Oahu, Hawaii. *Coral Reefs*, *12*(3-4), 177-184.

Jokiel P. L., Maragos J. E. (1978). Reef corals of Canton Atoll: II. Local distribution. In: Smith SV, Henderson RS, eds. *Phoenix Islands Report I. An environmental survey of canton atoll lagoon* 1973, Atoll Res. Bull. Washington D.C.: Smithsonian Institute. 221:73-97.

Jokiel, P. L., Rodgers, K. S., Brown, E. K., Kenyon, J. C., Aeby, G., Smith, W. R., & Farrell, F. (2015). Comparison of methods used to estimate coral cover in the Hawaiian Islands. *PeerJ,* 3, e954.

Lacks, A. (2000). *Reproductive Ecology and Distribution of the Scleractinian coral Fungia scutaria in Kane'ohe bay, O'ahu, Hawai'i*. (Masters thesis). University of Hawaii, Manoa.

Mayer, A. G. (1917). Is Death from High Temperature Due to the Accumulation of Acid in the Tissues?. *American Journal of Physiology-Legacy Content*, *44*(4), 581-585.

Maynard, J., Conklin, E. J., Minton, D., Most, R., Couch, C. S., Williams, G. J., ... & Martinez, J. (2016). Relative resilience potential and bleaching severity in the West Hawai'i Habitat Focus Area in 2015.

Möhlenkamp, P., Beebe, C., McManus, M., Kawelo, A., Kotubetey, K., Lopez-Guzman, M., ... & Alegado, R. (2019). Kū Hou Kuapā: Cultural Restoration Improves Water Budget and Water Quality Dynamics in Heʻeia Fishpond. *Sustainability*, *11*(1), 161.

Moberg, F., & Folke, C. (1999). Ecological goods and services of coral reef ecosystems. *Ecological Economics*, 29(2), 215-233.

Mouillot, D., Bellwood, D. R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., ... & Paine, C. T. (2013). Rare species support vulnerable functions in high-diversity ecosystems. *PLoS biology*, *11*(5), e1001569.

Mühlig-Hofmann, A. (2001). *The distribution of corals and macroalgae in relation to freshwater and sediment discharge on a fringing reef in Kane'ohe Bay, O'ahu, Hawai'i* (Masters thesis). University of Bremen, Germany.

Neilson, B. J., Wall, C. B., Mancini, F. T., & Gewecke, C. A. (2018). Herbivore biocontrol and manual removal successfully reduce invasive macroalgae on coral reefs. *PeerJ*, 6, e5332.

Price, N. (2010). Habitat selection, facilitation, and biotic settlement cues affect distribution and performance of coral recruits in French Polynesia. Oecologia, 163(3), 747-758.

Rodgers, S., & Cox, E. F. (1999). Rate of Spread of Introduced Rhodophytes Kappaphycus alvarezii, Kappaphycus striatum, and Gracilaria salicornia and Their Current Distribution in Kane'ohe Bay, O'ahu Hawai'i.

Rodgers, K. U. S., Jokiel, P. L., Brown, E. K., Hau, S., & Sparks, R. (2015). Over a decade of change in spatial and temporal dynamics of Hawaiian coral reef communities. *Pacific Science*, *69*(1), 1-13.

RStudio Team (2015). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/

Russell, D. J. (1983). Ecology of the imported red seaweed Eucheuma striatum Schmitz on Coconut Island, Oahu, Hawaii.

Smith, J. E., Hunter, C. L., Conklin, E. J., Most, R., Sauvage, T., Squair, C., & Smith, C. M. (2004). Ecology of the invasive red alga Gracilaria salicornia (Rhodophyta) on O'ahu, Hawai'i. *Pacific science*, *58*(2), 325-343.

Smith, S. V., Kimmerer W. J., Laws E. A., Brock R. E., & Walsh T. W. (1981). Kaneohe Bay Sewage diversion experiment: perspective, on ecosystem responses to nutritional perturbation. *Pac. Sci*, *35*, 279-395.

Stimson, J., & Conklin, E. (2008). Potential reversal of a phase shift: The rapid decrease in the cover of the invasive green macroalga Dictyosphaeria cavernosa Forsskål on coral reefs in Kāne ʻohe Bay, Oahu, Hawai ʻi. *Coral Reefs*, *27*(4), 717-726.

Stimson, J., Cunha, T., & Philippoff, J. (2007). Food preferences and related behavior of the browsing sea urchin Tripneustes gratilla (Linnaeus) and its potential for use as a biological control agent. *Marine Biology*, *151*(5), 1761-1772.

Stimson, J., Larned, S., & Conklin, E. (2001). Effects of herbivory, nutrient levels, and introduced algae on the distribution and abundance of the invasive macroalga Dictyosphaeria cavernosa in Kaneohe Bay, Hawaii. *Coral Reefs*, *19*(4), 343-357.

Stimson, J. (2018). Recovery of coral cover in records spanning 44 yr for reefs in Kāneʻohe Bay, Oaʻhu, Hawai ʻi. *Coral Reefs*, *37*(1), 55-69.

van Woesik, R., Sakai, K., Ganase, A., & Loya, Y. (2011). Revisiting the winners and the losers a decade after coral bleaching. *Marine Ecology Progress Series*, *434*, 67-76.

Wilkinson, C. (2000). *Status of coral reefs of the world: 2000*. Australian Institute of Marine Science.

Chapter 2

Reciprocal Transplant Demonstrates Acclimatization in *Porites compressa* and *Montipora capitata*, Kāneʻohe Bay, O’ahu

Kelsey A. Barnhill[1], Colleen N. Brown[2], Ashley E. McGowan[3], Keisha D. Bahr[4]

[1]Norwegian University of Life Sciences, [2]University of Miami, [3]Hawaiʻi Institute of Marine Biology, [4]Texas A&M University-Corpus Christi

Abstract

Coral reefs are susceptible to climate change, anthropogenic influence, and environmental stressors. However, corals in Kāneʻohe Bay have repeatedly shown resilience and the ability to acclimatize to climate change-induced rising temperatures and increased frequencies of bleaching events. A 2018 benthic survey completed on the Malauka`a fringing reef saw variations in coral and algal benthic cover at two sites just 600 meters apart from one another suggesting genetic and/or environmental differences in resilience between corals at the sites. A reciprocal transplant experiment was conducted to determine if calcification (linear extension and accretion) for the dominant reef-building corals *Montipora capitata* and *Porites compressa* varied between the two sites and whether or not genetics and/or environmental factors were responsible for the differences. The two sites represent distinct environmental conditions with significant differences between temperature, salinity, and aragonite saturation. Linear extension did not vary between sites for either species, suggesting the reef-building corals were able to acclimatize to the different environments. However, accretion (measured as change in mg g^{-1} d^{-1}) was significantly different between sites for *P. compressa*. Differences in accretion following transplantation suggest both environment and genetics impact secondary calcification of *P. compressa* in Kāneʻohe Bay.

Keywords acclimatization, calcification, coral reefs, reciprocal transplant, resilience

Introduction

Climate change-induced sea surface temperature increases and progressively frequent bleaching events threaten coral reef ecosystems globally (Hoegh-Guldberg et al., 2007, Hughes et al., 2017). Currently, many reefs are in decline as phase-shifts from coral-dominated to algae-dominated reefs occur (Bonaldo & Hay, 2014). Resilience of coral reefs to anthropogenic and environmental stressors is key to ensuring their longevity (Mumby et al., 2014). Some corals and coral reefs, for example, exhibit resilience through a natural resistance to bleaching (West & Salm, 2003). Additionally, individual corals are able to acclimatize to more frequent bleaching events (Coles & Brown, 2003) and survive to pass down their resistance, so the population can adapt and become more resilient (Baker et al., 2004; Pandolfi et al., 2011; Putnam et al., 2018).

While genotype and genetic variation can impact coral survivorship, environmental conditions also influence coral responses (e.g. growth, bleaching, etc.) (Drury et al., 2017).

The coral reefs in Kāneʻohe Bay, one of the most well-studied estuarine reef ecosystems, have shown resilience in response to various stressors (Bahr et al., 2015). Coral reefs in Kāneʻohe Bay have recovered from anthropogenic and environmental stressors such as sewage discharge (Pastorok & Bilyard, 1985), freshwater kills (Jokiel et al., 1993), and three major bleaching events (Bahr et al., 2017). The reefs in Kāneʻohe can be exposed to the air at low tides (Jokiel, 1991) and during summer months experience 1-2° Celsius elevated water temperatures- similar to middle/end of the century scenarios- which offshore reefs will not be exposed to for several years due to restricted flow (Bahr et al., 2015). Environmental disturbances, such as those in Kāneʻohe Bay, may allow for higher tolerance for bleaching (West & Salm, 2003). The resilience of the corals to environmental stressors as well as extreme temperatures (Bahr et al., 2015) makes Kāneʻohe Bay an ideal study site to explore responses of individual corals to different environmental conditions.

Following the most recent thermal-stress driven bleaching event in 2015, corals in different areas of the bay recovered at different rates (Bahr et al., 2017). A 2018 benthic survey completed on the Malauka`a fringing reef saw variations in benthic cover at two sites just 600 meters apart from one another (Barnhill, unpublished data). The northernmost 30 meters of the reef had 38.9% coral cover and 58.3% algae cover while the southernmost 30 meters of the reef had 62.5% coral cover and 25% algae cover (Barnhill, unpublished data). These observations led to the question of whether or not there were genetic differences influencing resilience between the corals in the bay, specifically at Malauka`a fringing reef.

In the era of molecular and genetic studies, common garden and reciprocal transplant experiments are often overlooked despite their ability to test whether or not local adaptations affect phenotypic traits (de Villemereuil et al., 2016). A reciprocal transplant experiment was used to test whether or not local adaptations and/or the environment influenced calcification differences between two sites. *Porites compressa* and *Montipora capitata* were the selected species for this experiment as they are the most common reef-building corals in Kāneʻohe Bay (Bahr et al., 2015). Calcification was the chosen parameter for measurements as Smith et al. (2016) suggests basing coral reef health on reef-building capacities of the corals, defining healthy reefs as those dominated by accreting and calcifying reef-building corals. Unhealthy, algae-dominated reefs show depressed calcification rates compared to coral-dominated reefs (Gattuso et al., 1998) and temperature-induced bleaching can decrease or halt calcification rates (Carilli et al., 2009), which must remain above the rate of erosion/dissolution to maintain coral cover and net accretion (Gattuso et al., 1998). The objectives of this experiment were to 1.) determine if *M. capitata* and *P. compressa* were calcifying at different rates between the two sites and if so, 2.) determine if environment or genetics explained the differences in calcification between sites.

Methods

Study Site

This research was conducted in Kāne‘ohe Bay, Hawai‘i (21.4°N, 157.8°W). A barrier reef separates the ocean from the inshore Kāne‘ohe Bay estuarine system which is characterized by numerous shallow patch reefs (<1 meter depth) and a shallow fringing reef (0.3-0.9 meters depth) ringing the majority of the shoreline (Jokiel, 1991). Reefs in the bay have one of the highest percentages of coral cover (54-68%) among the Hawaiian islands (Hawaii average = 24.1%) (Bahr et al., 2017; Jokiel et al., 1993; Rodgers et al., 2015). Site 1 (21.44300899°N, -157.80636°W) was located approximately 125 meters offshore of Kealohi Point at He’eia State park. Site 2 (21.43853104°N, -157.806541°W) was located just 25 meters away from the Paepae o He‘eia (He’eia traditional Hawaiian fishpond), directly in front of a triple mākāhā (sluice gate). Both sites were located on the inshore edge of Malauka`a fringing reef (Figure 1).

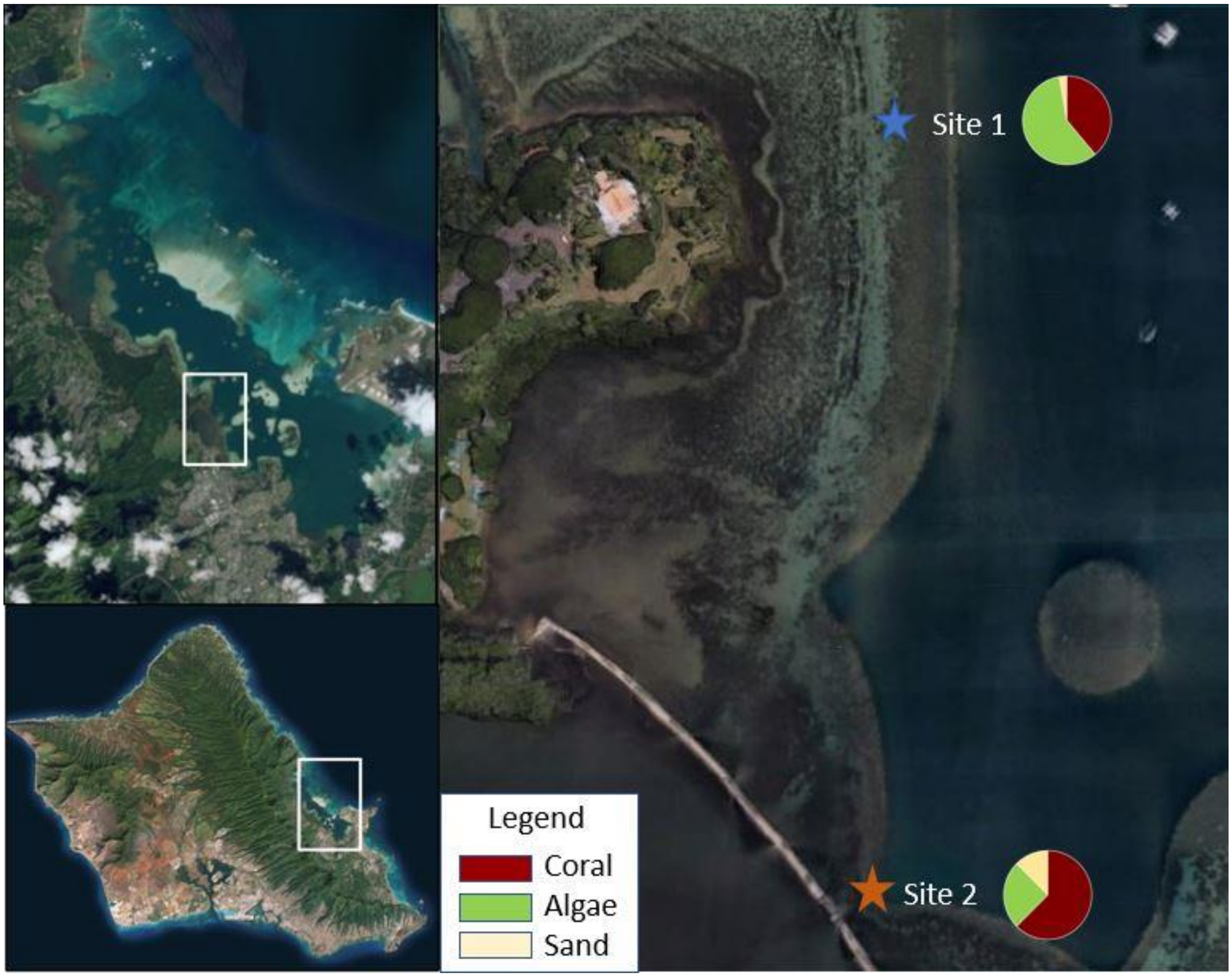


Figure 1. Map of Malauka`a fringing reef situated in Kāne‘ohe Bay, O’ahu with site 1 and site 2 identified and benthic cover described. Picture credit: Digital Globe & Google Earth.

Environmental Parameters

Temperature (°C) at the two sites was recorded continuously during the experimental period (50 days) using Hobo Pro V2 temperature loggers (Onset Computer Corporation). Sedimentation (mg cm^2 hr^1) was measured five separate times during quarterly sampling from May 2017-June 2018 by deploying two sediment traps at each site for 24 hours. Preliminary nutrient data (i.e. Nitrogen, Phosphorous, Phosphate, Silicate, and Ammonia) (µmol L^1) was taken during three quarterly samplings in September 2017, December 2017, and March 2018. Salinity (ppt), turbidity (NTU), pH, and Aragonite saturation (ΩArag) were recorded during preliminary seawater chemistry sampling over two 12-hour cycles in July 2018. Salinity was recorded using an YSI 556 MPS (Xylem Analytics) and turbidity was measured using a 2100Q Portable Turbidimeter (Hach). Some additional turbidity measurements were collected during the experimental period (June-July 2018). Optical pH measurements were made with m-cresol purple dye using an on-site LC Mass Spectrometer. Two or more analyses were done for each sample to reach a standard deviation of 0.01 or less. ΩArag was calculated from pH and Total Alkalinity values using the CO2SYS V2.1 Calc program for Excel Pierrot).

Experimental Setup

Colonies of *Porites compressa* (n = 5) and *Montipora capitata* (n = 5) were collected at each site (with ~35 m of the site) at approximately 1 m depth and fragmented into coral nubbins (six nubbins per colony) of comparable size (11.66 g ± 2.95) for a total of 120 nubbins of *P. compressa* (n = 60) and *M. capitata* (n = 60).

Coral nubbins were tagged and affixed onto ceramic pedestals in an upright position and placed on a tray. Thirty nubbins of each species were randomly selected to either stay at their own site (‘Site 1 resident’: coral nubbin originally from site 1 which remained at site 1 during the experiment) or be transplanted to the other site (‘Site 1 transplant’: coral nubbin originally from site 2 which was transplanted to site 1 during the experiment). One nubbin per colony was placed on each tray to avoid pseudoreplication. The experiment took place over 50 days (11 June- 31 July) during the summer of 2018. Extension and accretion were the selected parameters to monitor coral calcification. Corals with high levels of partial mortality (>80% tissue loss) at the end of the 50-day period were removed from calcification analysis.

Coral Growth Measurements: Extension

To measure linear extension rates, nubbins were stained before the start of the experiment using the Alizarin sodium monosulfonate (hereafter Alizarin) technique (Barnes, 1970). Coral nubbins were stained in an aerated 475-liter tank with Alizarin concentration at 15 ppm for 8 hours in direct sunlight (Rodgers & Cox, 2003). Corals were unharmed during the staining process as Alizarin concentrations below 20 ppm are not damaging (Lamberts, 1973). After the conclusion of the 50-day experiment, all nubbins were exposed to a mixture of freshwater and bleach for 12 hours to remove tissue and expose the stained skeleton. Calipers were used to measure coral skeletal growth from the stain to the point of maximum linear growth in mm to 1 decimal point (Figure 2). If a nubbin had multiple branches, maximum linear growth was measured for each branch, and the mean value was recorded. All linear extension values were converted to mm d^{-1}

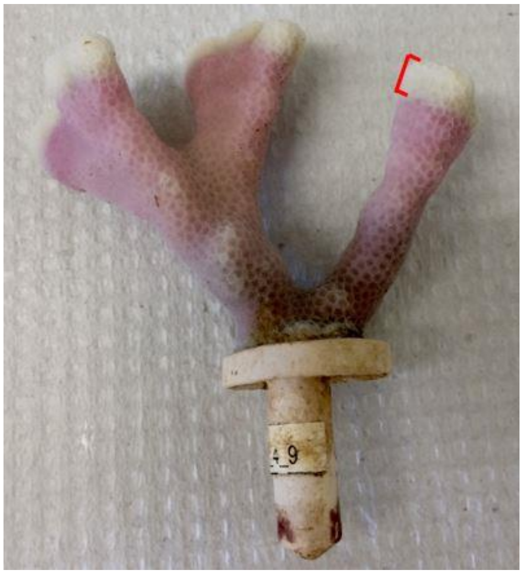


Figure 2. A stained *P. compressa* nubbin's exposed skeleton. Linear extension was measured from the stain up to the white growth tip. Picture credit: Kelsey Barnhill.

Coral Growth Measurements: Accretion

To measure coral accretion rates, each nubbin was weighed using the buoyant weight technique (Jokiel et al., 1978) before the start of the experiment and at the end of the 50-day experiment. Values were converted to dry skeletal weight (Jokiel, et al., 1978) and percent change in mg g^{-1} d^{-1} was calculated.

Statistical Analysis

The effects of the resident and transplant sites on calcification (i.e. accretion and linear extension) for each species was determined using a Type II ANOVA. Post-hoc pairwise comparison (Tukey, 95% CI) was used to determine differences in coral growth between sites for each species. Environmental conditions (i.e., temperature, salinity, turbidity, sedimentation, pH and ΩArag) between site 1 and site 2 were analyzed using two-tailed paired T-tests. A Bonferroni correction was used to counteract the multiple tests (n = 6) between environmental parameters. The relationship between accretion and extension was fitted using a linear regression. Assumptions of normal distribution and homoscedasticity were assessed through graphical analysis of the residuals. Descriptive and statistical analyses were conducted using R

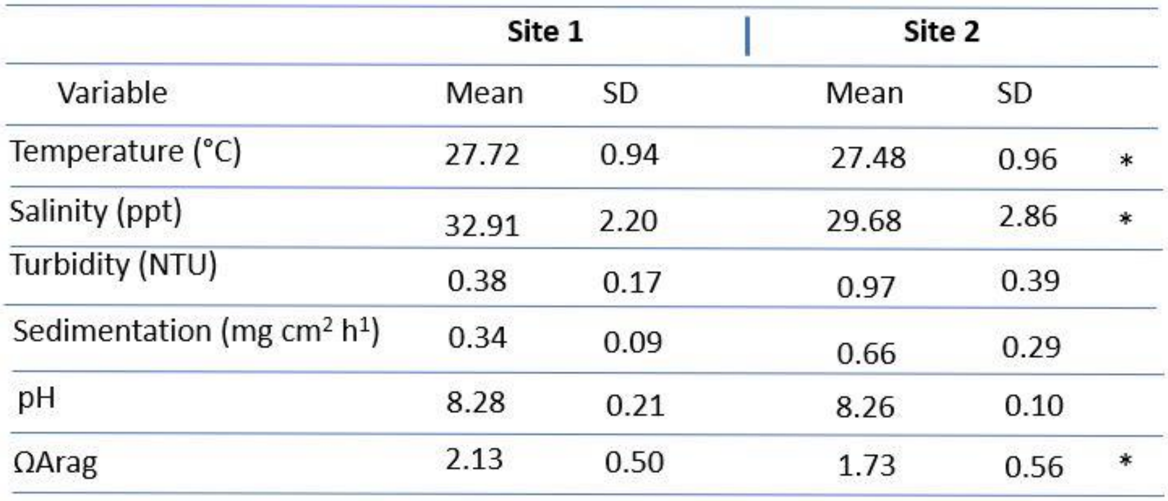
Commander (Fox & Bouchet-Valat, 2019). Graph of mean accretion rates was created using JMP 13 Pro (SAS Institute Inc., USA).

Results

Environmental Parameters

Midday (11:00-14:00) temperature (°C) (mean ± SD) was 27.72 ± 0.94 at site 1 and 27.48 ± 0.96 at site 2 ($p < 0.0001$) (Table 1). Temperatures ranged from 25.89°C to 31.94°C at site 1 and 25.67°C to 30.72°C at site 2 during the 50-day experiment. The mean salinity (ppt) was 32.91 ± 2.20 at site 1 and 29.68 ± 2.86 at site 2 ($p = 0.0037$). The mean turbidity (NTU) was 0.38 ±0.17 at site 1 and 0.97 ±0.39 at site 2 ($p = 0.011$). The mean sedimentation (mg cm^{2} hr^{1}) was 0.34 ± 0.09 at site 1 and 0.66 ± 0.29 at site 2 ($p = 0.078$). The mean pH was 8.28 ± 0.21 at site 1 and 8.26 ± 0.10 at site 2 ($p = 0.744$). The mean ΩArag was 2.13 ± 0.50 at site 1 and 1.73 ± 0.56 at site 11 ($p = 0.0079$). The average of three nutrient samplings for Nitrogen, Phosphorus, Phosphate, Silicate, and Ammonia (µmol L^{1}) was 5.88, 0.33, 0.19, 10.34, and 0.45 respectively, for site 1 and 7.11, 0.37, 0.16, 21.07, and 0.71, respectively for site 2.

Table 1. Environmental Parameters for each site. * Indicates significant difference at Bonferroni corrected $p < 0.008$



	Site 1		Site 2		
Variable	Mean	SD	Mean	SD	
Temperature (°C)	27.72	0.94	27.48	0.96	*
Salinity (ppt)	32.91	2.20	29.68	2.86	*
Turbidity (NTU)	0.38	0.17	0.97	0.39	
Sedimentation (mg cm^{2} h^{1})	0.34	0.09	0.66	0.29	
pH	8.28	0.21	8.26	0.10	
ΩArag	2.13	0.50	1.73	0.56	*

Relationship between Extension and Accretion

The regression line for extension and accretion was $y = 1.0224 + 0.6268x$ with an R^2 value of 0.317 for *M. capitata* and $y = 1.5012 + 0.6305x$ with an R^2 value of 0.358 for *P. compressa* (Figure 3).

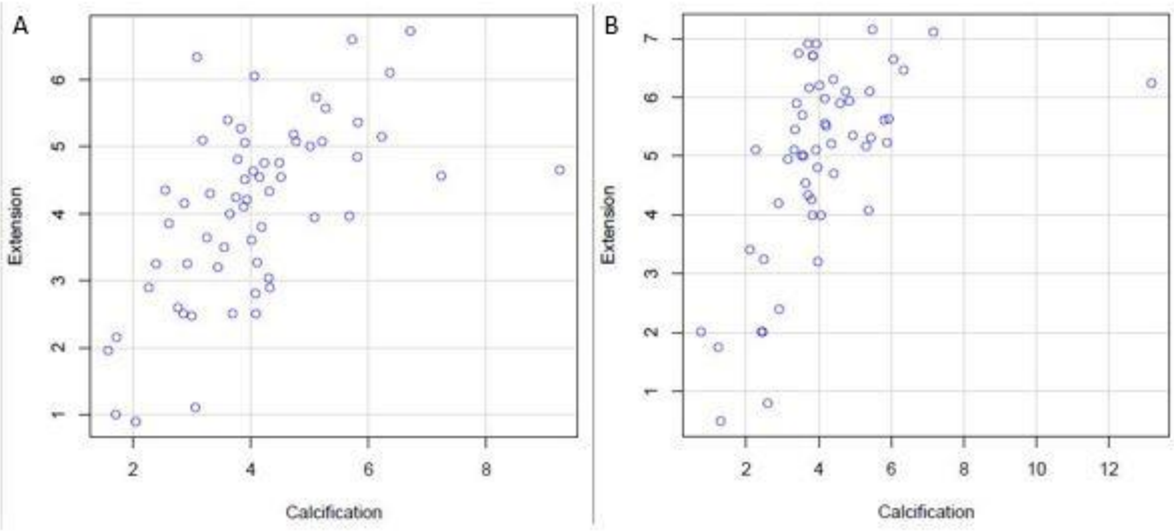
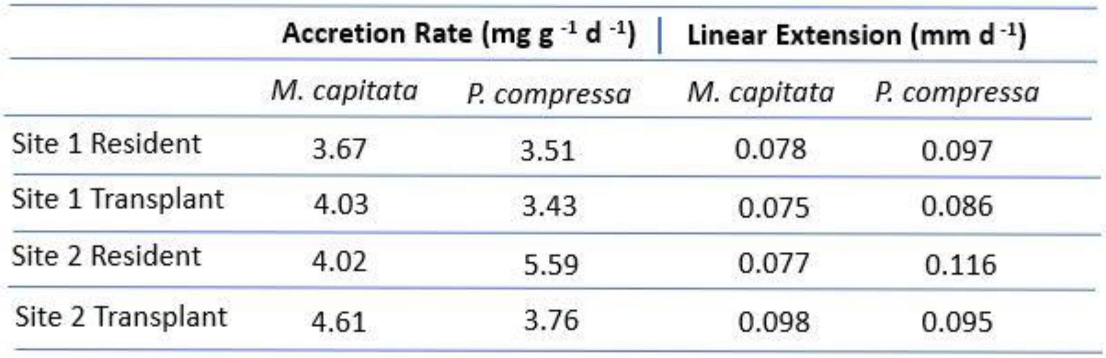


Figure 3. Linear regression showing the relationship between extension and calcification for A) *M. capitata* and B) *P. compressa*..

Coral Growth Measurements: Extension

Mean extension rates were similar for each species across sites. The mean extension rate for *M. capitata* was 0.076 ± 0.026 mm d^{-1} for site 1 and 0.087 ± 0.027 mm d^{-1} at site 2 ($p = 0.123$) while the mean extension rate for *P. compressa* was 0.091 ± 0.032 mm d^{-1} for site 1 and 0.106 ± 0.032 mm d^{-1} for site 2 ($p = 0.137$) (Table 2). Neither Resident nor Transplantation site had an effect on extension rates.

Table 2. Mean linear extension and accretion rates for resident and transplant *M. capitata* and *P. compressa* coral nubbins at each site.

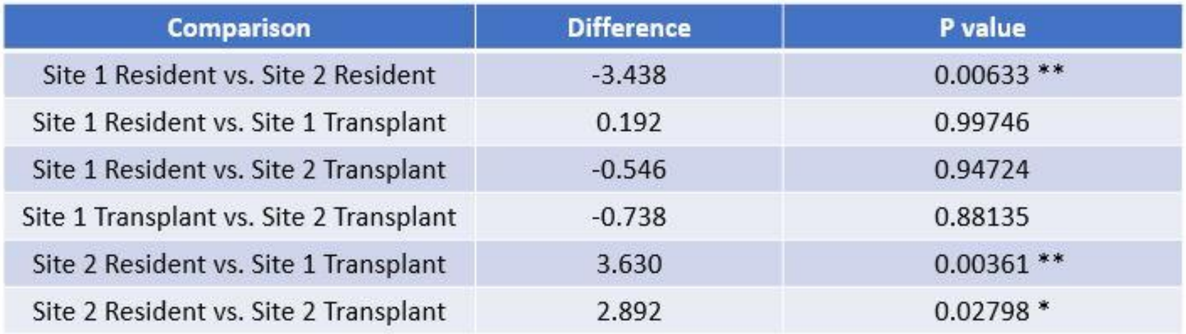


	Accretion Rate (mg g $^{-1}$ d $^{-1}$)		**Linear Extension (mm d $^{-1}$)**	
	M. capitata	*P. compressa*	*M. capitata*	*P. compressa*
Site 1 Resident	3.67	3.51	0.078	0.097
Site 1 Transplant	4.03	3.43	0.075	0.086
Site 2 Resident	4.02	5.59	0.077	0.116
Site 2 Transplant	4.61	3.76	0.098	0.095

Coral Growth Measurements: Accretion

Montipora capitata had a mean accretion rate of 4.082 ± 1.408 mg g $^{-1}$ d $^{-1}$ and did not show any significant differences in accretion between sites. Neither the original site nor the transplant site impacted accretion rates for *M. capitata*, however both variables significantly impacted accretion of *P. compressa* ($p = 0.028$, 0.005, respectively). *Porites compressa* showed a significant difference in calcification accretion rates between sites. Site 1 residents had significantly lower accretion rates (mean ± SD) (3.51 ± 0.70 mg g^{-1} d^{-1}) compared to site 2 residents (5.05 ± 1.19 mg g^{-1} d^{-1}) ($p = 0.006$). *Porites compressa* site 2 transplants had a mean accretion rate of 3.757 ± 1.187 mg g^{-1} d^{-1}while site 1 transplants had a mean accretion rate of 3.426 ± 1.343 mg g^{-1} d^{-1}. Both site 1 transplants and site 2 transplants had significantly reduced accretion rates compared to site 2 residents ($p = 0.004$, 0.028, respectively) (Table 3 & Figure 4).

Table 3. Multiple comparisons of accretion rates between resident and transplant sites for *P. compressa.* * Indicates a significant response at $p < 0.05$ ** Indicates significant response at $p < 0.01$



Comparison	Difference	P value
Site 1 Resident vs. Site 2 Resident	-3.438	0.00633 **
Site 1 Resident vs. Site 1 Transplant	0.192	0.99746
Site 1 Resident vs. Site 2 Transplant	-0.546	0.94724
Site 1 Transplant vs. Site 2 Transplant	-0.738	0.88135
Site 2 Resident vs. Site 1 Transplant	3.630	0.00361 **
Site 2 Resident vs. Site 2 Transplant	2.892	0.02798 *

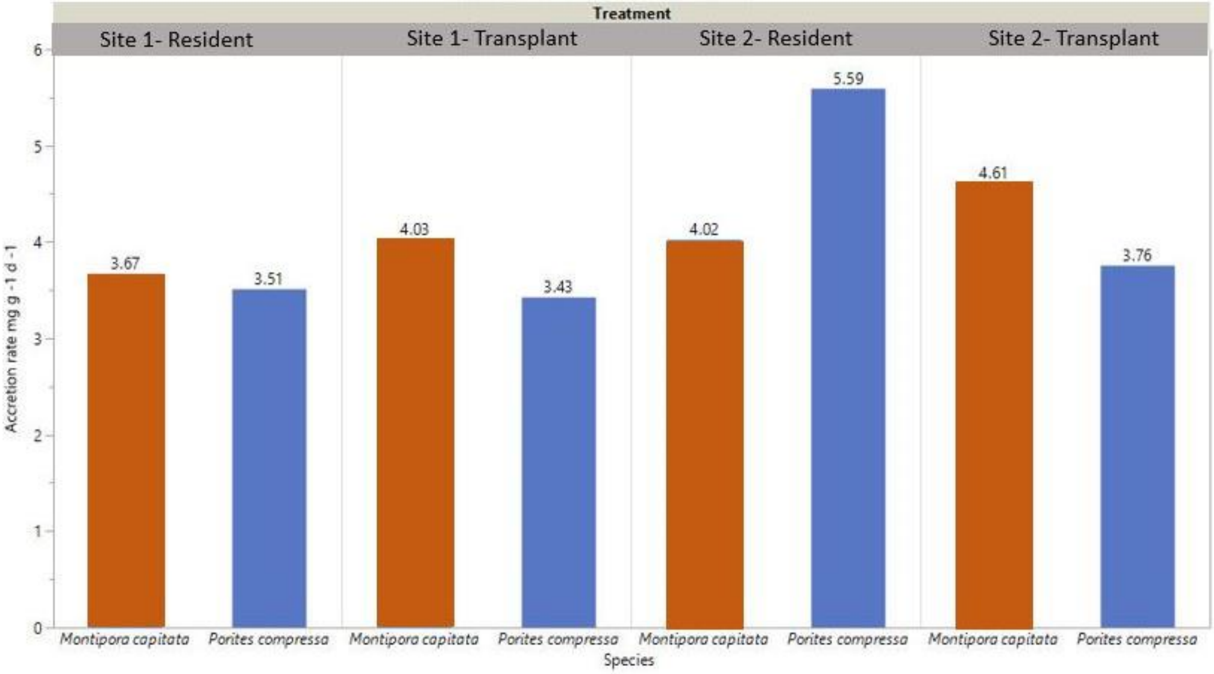


Figure 4. Accretion rates (mg g^{-1} d^{-1}) for resident and transplant *M. capitata* and *P. compressa* nubbins at both sites.

Discussion

Differences in coral percent cover between sites at the Malauka`a fringing reef could be caused by environmental differences between sites, genetic variations in individual corals, or a combination of the two. Calcification differences between populations of each species at the two sites during the reciprocal transplant could indicate genetic-based coral resilience (Barshis et al., 2013).

Corals at the two sites experienced different environmental conditions during the experiment as there were significant differences in temperature, salinity, and ΩArag between sites. The mid-day average temperature experienced by corals at site 1 was 0.24°C higher than the average temperature experienced by corals at site 2. Additionally, corals at site 1 experienced two days with temperatures above the upper thermal threshold for Hawaiian corals (31°C) (Jokiel & Coles, 1974; Jokiel & Coles, 1977) while the maximum temperature reached at site 2 was 30.72°C.

Salinities were also significantly different between the two sites. At site 1 the mean salinity (32.91 ppt) was significantly higher than at site 2 (29.68 ppt). The lower salinity at site 2 was likely caused by freshwater input from He’eia stream and Paepae o He‘eia. Site 2 also experienced greater fluctuations in salinity levels with higher salinities during flood tides (maximum salinity observed = 33.01) and lower levels during ebb tides (minimum salinity observed = 23.7), as water from Paepae o He‘eia flowed out of the triple mākāhā onto the site. While the average salinity at each site was within tolerable levels for coral reefs (> 25 ppt , < 45 ppt) salinity at site 2 was below the previously recorded salinity range for Kāne‘ohe Bay of 30.9-36.2 (Coles & Jokiel, 1992). Site 2’s historically low salinity may be attributed to Paepae o He‘eia biocultural restoration (e.g. fishpond wall repair, alien mangrove removal) as a mean 5802 m^3 of water flowed onto the reef during each ebb tidal cycle pre-restoration (2012) compared to 20220 m^3 in 2018 (Möhlenkamp et al., 2019).

Based on two days of 12-hour cycle preliminary carbonate chemistry sampling, the ΩArag levels appear to be different between sites as well. Mean ΩArag levels at both sites (2.13, 1.73, respectively) were significantly lower than the 1998 global average of 3.8, as well as the global minimum mean of 3.3 (Kleypas et al., 1999). Guinotte et al., (2003) stated that ΩArag levels are above 3.0 for all prominent reef ecosystems, however, since then, inshore reefs have been found capable to continue growing in ΩArag levels below what was once predicted as detrimental to coral health (Uthicke, 2014).

pH at both sites (8.28, 8.26 at site 1 and 2, respectively) was within mean pH value measurements at coral reefs (Ningaloo reef = 8.22-8.64, Great Barrier reef = 7.98-8.37, Media Luna reef (Puerto Rico) = 8.01-8.09) (Gagliano, et al., 2010; Gray et al., 2012). While the mean sedimentation (mg cm^2 hr^1) rates were not significantly different from one another between sites (0.34, 0.66 at sites 1 and 2, respectively) the rate seen at site 1 is within mean rates for reefs not greatly impacted by human development, while the rate at site 2 implies sedimentation has been anthropogenically-elevated (Rogers, 1990). Turbidity (NTU) was also similar between sites (0.38, 0.97 at sites 1 and 2, respectively) and was within mean turbidity levels seen at the Great Barrier Reef (Fabricius, et al., 2013).

Preliminary nutrient data suggests there may be further differences between sites. Values of Nitrogen and Silicate (μmol L^1) were higher at site 2 (7.11, 21.07) than site 1 (5.88, 10.34). These elevated nutrient levels at site 2 were likely caused by input from He'eia stream and Paepae o Heʻeia. Enriched Nitrogen levels can reduce calcification rates in corals by up to 50%, however these reductions are seen at higher Nitrogen concentrations (20 μmol L^1) than observed at either site (Kinsey & Davies, 1979; Fabricius, 2005)

Calcification is a good indicator of coral health as up to 30% of a coral's energy is allocated to calcification (Allemand et al., 2011). Extension is characterized by low-density, fast upward growth at the tips and can be referred to as primary calcification (Gladfeiter, 1982). Accretion follows extension and is a slower, outward growth from the sides of the coral, also referred to as secondary calcification (Gladfeiter, 1982). Through measuring extension and accretion, the results of this study explored both primary and secondary calcification. Extension and accretion did not show a strong correlation (R^2 of 0.317 and 0.358 for *M. capitata* and *P. compressa*, respectively) indicating that the two growth mechanisms occur at different time scales for these species (Jokiel et al., 2016). The low R^2 value for the relationship between extension and accretion for both species corroborates the findings of Dodge & Brass (1984) who suggest measuring one parameter alone is insufficient to describe coral growth. Secondary calcification in *P. compressa* was affected more than primary calcification as there were significant differences in accretion rates between sites whereas the linear extension rate did not differ.

Primary calcification for both species were similar to rates in Kāneʻohe Bay quantified by Cox (1986) and Grottoli (1999). Neither the original site (genetic legacies) nor the transplant site (environmental influences) impacted extension rates of either species of coral. The similarity in extension rates for both species between sites indicates that the transplanted corals were able to acclimatize to their new environment and continue to extend upwards at the same rate.

M. capitata accretion rates (4.082 ± 1.408 mg g^{-1} d^{-1}) were higher than the previous maximum of 3.5 mg g^{-1} d^{-1} seen in Kāneʻohe Bay (Jokiel & Coles, 1977). Accretion rates in *M. capitata* did not vary between sites or treatments implying that the species may be relatively tolerant of environmental stressors. The consistency between sites also shows that *M. capitata* is able to quickly acclimatize to new environments, including environments with thermal stressors and low ΩArag levels, as linear extension and accretion of both transplanted groups did not differ from residents.

Both the environment ($p = 0.005$) and individual traits ($p = 0.028$) of each colony affected accretion for *P. compressa*, though the environment had a larger effect. This indicates secondary calcification of *P. compressa* in Kāneʻohe Bay is influenced by the interaction of environmental conditions and colony genetics. This finding is further supported by the results of the multiple comparisons test (Table 3). Through the multiple comparisons test, secondary calcification of *P. compressa* between site 1 and site 2 residents was significantly different. The secondary calcification was significantly different between nubbins which remained at Site 2 and those which were transplanted to Site 1, indicating environment determines growth rates. However, as secondary calcification rates were also significantly different between Site 2 resident nubbins and the Site 2 transplant nubbins, colony genetics also affects growth. Aside from population-wide acclimatization trends, variation occurred at the individual level as well. Two out of three nubbins from the same colony of *P. compressa* died at the site 1 control treatment, while the third nubbin suffered 50% mortality with the remaining 50% pale. Future studies should further explore responses of individuals from the same colony to better understand genetic influence to acclimatization and resilience.

P. compressa's survivorship and calcification rates have previously been found to be highly susceptible to temperature and acidification stressors, indicating the species is sensitive to changes in environmental conditions (Bahr et al., 2016). The significantly higher temperatures at site 1 likely decreased accretion rates of *P. compressa*. Accretion rate was higher at site 2 despite its depressed salinity values (minimum observed = 23.7 ppt) and low ΩArag (Minimum observed = 1.19). While calcification rates can be affected by different environmental conditions (e.g. nutrient levels, light, ΩArag, etc.) temperature has been found to be particularly important (Carricart-Ganivet et al., 2012; Jokiel & Coles, 1977). Calcification rates for *Porites* spp. are sensitive to thermal stress as a 1°C increase in temperature decreases calcification rates by 0.40 g cm^{-2} yr^{-1}(Carricart-Ganivet et al., 2012) and a 2.8°C increase can reduce calcification rates in P. compressa by 51% (Coles et al., 2018). The increased availability of nutrients at site 2 likely also impacted calcification rates. The changes in accretion between sites thus corroborates previous findings that *P. compressa* is sensitive to environmental changes.

The major finding that both environment and genetics influence *P. compressa*'s secondary calcification rates in Kāneʻohe Bay has management implications. It is important to not only consider the environment when modeling coral responses to stressors, but also the genetic legacies of the corals.

Author Contributions

Kelsey A. Barnhill conceived and designed the experiment, performed the experiment, collected data, analyzed the data, prepared figures and/or tables, and authored drafts of the paper.
Colleen N. Brown collected data and analyzed the carbonate data.
Ashley E. McGowan performed the experiment and collected data.
Keisha D. Bahr conceived and designed the experiment, contributed reagents/materials/analysis tools and reviewed/edited drafts of the paper.

Reference List

Allemand, D., Tambutté, É., Zoccola, D., & Tambutté, S. (2011). Coral calcification, cells to reefs. In *Coral reefs: an ecosystem in transition* (pp. 119-150). Springer, Dordrecht.

Bahr, K. D., Jokiel, P. L., & Rodgers, K. (2016). Relative sensitivity of five Hawaiian coral species to high temperature under high-pCO 2 conditions. *Coral Reefs*, 35(2), 729-738.

Bahr, K. D., Jokiel, P. L., & Toonen, R. J. (2015). The unnatural history of Kāne ʻohe Bay: coral reef resilience in the face of centuries of anthropogenic impacts. *PeerJ*, *3*, e950.

Bahr, K. D., Rodgers, K. S., & Jokiel, P. L. (2017). Impact of Three Bleaching Events on the Reef Resiliency of Kāneʻohe Bay, Hawaiʻi. *Frontiers in Marine Science, 4*, 398.

Baker, A. C., Starger, C. J., McClanahan, T. R. & Glynn, P. W. (2004). Coral reefs: corals' adaptive response to climate change. *Nature 430*, 741–741.

Barnes, D.J. (1970). Coral skeletons: an explanation of their growth and structure. *Science*, *170*(3964), 1305-1308.

Barshis, D. J., Ladner, J. T., Oliver, T. A., Seneca, F. O., Traylor-Knowles, N., & Palumbi, S. R. (2013). Genomic basis for coral resilience to climate change. *Proceedings of the National Academy of Sciences*, *110*(4), 1387-1392.

Bonaldo, R. M., & Hay, M. E. (2014). Seaweed-coral interactions: variance in seaweed allelopathy, coral susceptibility, and potential effects on coral resilience. *PloS one*, *9*(1), e85786.

Carilli, J. E., Norris, R. D., Black, B. A., Walsh, S. M., & McField, M. (2009). Local stressors reduce coral resilience to bleaching. *Plos one*, *4*(7), e6324.

Carricart-Ganivet, J. P., Cabanillas-Teran, N., Cruz-Ortega, I., & Blanchon, P. (2012). Sensitivity of calcification to thermal stress varies among genera of massive reef-building corals. *PLoS One*, *7*(3), e32859.

Coles, S. L., Bahr, K. D., Ku'ulei, S. R., May, S. L., McGowan, A. E., Tsang, A., ... & Han, J. H. (2018). Evidence of acclimatization or adaptation in Hawaiian corals to higher ocean temperatures. PeerJ, 6, e5347.

Coles, S. L., & Brown, B. E. (2003). Coral bleaching—capacity for acclimatization and adaptation. Advances in Marine Biology, 46, 183-223.

Coles, S. L., & Jokiel, P. L. (1992). Effects of salinity on coral reefs. *Pollution in tropical aquatic systems*, 147-166.

Cox, E. F. (1986). The effects of a selective corallivore on growth rates and competition for space between two species of Hawaiian corals. *Journal of Experimental Marine Biology and Ecology*, *101*(1-2), 161-174.

de Villemereuil, P., Gaggiotti, O. E., Mouterde, M., & Till-Bottraud, I. (2016). Common garden experiments in the genomic era: new perspectives and opportunities. *Heredity*, *116*(3), 249.

Dodge, R.E., & Brass, G.W. (1984). Skeletal extension, density and calcification of the reef coral, Montastrea annularis: St. Croix, US Virgin Islands. *Bulletin of Marine Science, 34*(2), 288-307.

Drury, C., Manzello, D., & Lirman, D. (2017). Genotype and local environment dynamically influence growth, disturbance response and survivorship in the threatened coral, Acropora cervicornis. *PloS one*, *12*(3), e0174000.

Fabricius, K. E. (2005). Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine pollution bulletin*, *50*(2), 125-146.

Fabricius, K. E., De'ath, G., Humphrey, C., Zagorskis, I., & Schaffelke, B. (2013). Intra-annual variation in turbidity in response to terrestrial runoff on near-shore coral reefs of the Great Barrier Reef. *Estuarine, Coastal and Shelf Science*, *116*, 57-65.

Fox, J., & Bouchet-Valat, M. (2019). Rcmdr: R Commander. R package version 2.5-2.

Gray, S. E., DeGrandpre, M. D., Langdon, C., & Corredor, J. E. (2012). Short-term and seasonal pH, pCO2and saturation state variability in a coral-reef ecosystem. *Global Biogeochemical Cycles*, *26*(3).

Gagliano, M., McCormick, M. I., Moore, J. A., & Depczynski, M. (2010). The basics of acidification: baseline variability of pH on Australian coral reefs. *Marine Biology*, *157*(8), 1849-1856.

Gladfeiter, E. H. (1982). Skeletal development in Acropora cervicornis: I. Patterns of calcium carbonate accretion in the axial corallite. *Coral reefs*, *1*(1), 45-51.

Grottoli, A. G. (1999). Variability of stable isotopes and maximum linear extension in reef-coral skeletons at Kaneohe Bay, Hawaii. *Marine Biology*, *135*(3), 437-449.

Guinotte, J. M., Buddemeier, R. W., & Kleypas, J. A. (2003). Future coral reef habitat marginality: temporal and spatial effects of climate change in the Pacific basin. *Coral reefs*, *22*(4), 551-558.

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., ... & Knowlton, N. (2007). Coral reefs under rapid climate change and ocean acidification. *Science*, *318*(5857), 1737-1742.

Hughes, T. P., Kerry, J. T., Álvarez-Noriega, M., Álvarez-Romero, J. G., Anderson, K. D., Baird, A. H., ... & Bridge, T. C. (2017). Global warming and recurrent mass bleaching of corals. *Nature*, *543*(7645), 373.

Jokiel, P. L. (1991). *Jokiel's illustrated scientific guide to Kāneʻohe Bay*.

Jokiel, P. L., & Coles, S. L. (1974). Effects of heated effluent on hermatypic corals at Kahe Point, Oahu. *Pacific Science, 28(1)*.

Jokiel, P. L., & Coles, S. L. (1977). Effects of temperature on the mortality and growth of Hawaiian reef corals. *Marine Biology*, *43*(3), 201-208.

Jokiel, P. L., Hunter, C. L., Taguchi, S., & Watarai, L. (1993). Ecological impact of a fresh-water "reef kill" in Kaneohe Bay, Oahu, Hawaii. *Coral Reefs*, *12*(3-4), 177-184.

Jokiel, P. L., Jury, C. P., & Kuffner, I. B. (2016). Coral calcification and ocean acidification. In *Coral reefs at the crossroads* (pp. 7-45). Springer, Dordrecht.

Jokiel, P. L., Maragos, J.E., & Franzisket, L. (1978). Coral growth: buoyant weight technique. In: Johannes, D.R., ed. *Coral Reefs: research methods, monographs on oceanographic methodology*. Paris: UNESCO. 529-542.

Kinsey, D. W., & Davies, P. J. (1979). Effects of elevated nitrogen and phosphorus on coral reef growth 1. *Limnology and oceanography*, *24*(5), 935-940.

Kleypas, J. A., McManus, J. W., & Menez, L. A. (1999). Environmental limits to coral reef development: where do we draw the line?. *American Zoologist*, *39*(1), 146-159.

Lamberts, A. E. (1973). *Alizarin deposition by corals* (Doctoral dissertation) University of Hawaii, Honolulu.

Möhlenkamp, P., Beebe, C., McManus, M., Kawelo, A., Kotubetey, K., Lopez-Guzman, M., ... & Alegado, R. (2019). Kū Hou Kuapā: Cultural Restoration Improves Water Budget and Water Quality Dynamics in Heʻeia Fishpond. *Sustainability*, *11*(1), 161.

Mumby, P. J., Wolff, N. H., Bozec, Y. M., Chollett, I., & Halloran, P. (2014). Operationalizing the resilience of coral reefs in an era of climate change. *Conservation Letters*, *7*(3), 176-187.

Pandolfi, J. M., Connolly, S. R., Marshall, D. J., & Cohen, A. L. (2011). Projecting coral reef futures under global warming and ocean acidification. *Science*, *333*(6041), 418-422.

Pastorok, R. A., & Bilyard, G. R. (1985). Effects of sewage pollution on coral-reef communities. *Marine ecology progress series. Oldendorf*, *21*(1), 175-189.

Pierrot, D., Lewis, D. E., and Wallace, D. W. R.: MS Excel Program Developed for CO2 System Calculations, ORNL/CDIAC-105a, Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tennessee, https://doi.org/10.3334/CDIAC/otg.CO2SYS_XLS_CDIAC105a, 2006.

Putnam, H. M., Ritson-Williams, R., Cruz, J. A., Davidson, J. M., & Gates, R. D. (2018). Nurtured by nature: Considering the role of environmental and parental legacies in coral ecological performance. *bioRxiv*, 317453.

Rodgers, KS., & Cox, E. F. (2003). The effects of trampling on Hawaiian corals along a gradient of human use. *Biological Conservation*, *112*(3), 383-389.

Rodgers, K. S., Jokiel, P. L., Brown, E. K., Hau, S., & Sparks, R. (2015). Over a decade of change in spatial and temporal dynamics of Hawaiian coral reef communities. *Pacific Science, 69*(1), 1-13.

Rogers, C. S. (1990). Responses of coral reefs and reef organisms to sedimentation. *Marine ecology progress series. Oldendorf*, *62*(1), 185-202.

Smith, J. E., Brainard, R., Carter, A., Grillo, S., Edwards, C., Harris, J., ... & Vroom, P. S. (2016). Re-evaluating the health of coral reef communities: baselines and evidence for human impacts across the central Pacific. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1822), 20151985.

West, J. M., & Salm, R. V. (2003). Resistance and resilience to coral bleaching: implications for coral reef conservation and management. *Conservation Biology*, *17*(4), 956-967.

Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway