Spatial and temporal trends of *Acropora* and *Porites* coral assemblages across Micronesia

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Abstract

Coral reefs are diverse ecosystem that provide many essential goods and services to Micronesian communities. Over the past few decades Micronesian coral reefs have been exposed to a variety of stressors which have caused rapid ecological change. For example, Degree Heating Week (DHW) events, a metric for thermal stress, were rare in Micronesia's past. However, in 2016-2017 the region experienced its first significant DHW events which led to extensive coral mortality throughout the region. While it is generally recognized that these climate-induced and localized anthropogenic stressors are shifting coral reef assemblages from sensitive to more stress tolerant species, less is known about the rates of change, spatial patterns, and specific drivers behind this process. This thesis focused on two prominent coral genera, *Acropora* and *Porites*, due to their significance to coral reefs and contrasting life histories. Historic data revealed that in the 1980s *Acropora* corals were ubiquitous across reef types and geographic scales with predominantly large arborescent and plating growthforms, that provided important structural complexity, fast growth, and fish habitat across Micronesia. However, many reefs once dominated by *Acropora* have been shifting to *Porites* across decades, contextually, based upon their exposure to wave energy and local stressors. For example, between the 1980s and the mid 2010s there had been a separation of outer reefs into two distinct coral communities: leeward reefs dominated by *Porites* and windward reefs dominated by *Acropora*, whereas inner fringe and patch/back reefs continued to increase in *Porites* dominance over this same timeframe. Most recently, climate change related DHW stress events were shown to negatively impact both *Acropora* and *Porites*, however, the resistance and susceptibly of both genera was contextual based on intensity of the event and spatial distribution. For example, through the more intense DHW events (DHW>10) in 2016-2017, the largest remaining populations of *Acropora* cover were heavily impacted on windward outer reefs (mean relative change -62.9%) and on patch/back reefs (mean relative change -48.9%), and the once common large *Acropora* growth forms, the arborescent and plates, had virtually disappeared across all reef types. Conversely, through these same DHW events *Porites* cover was particularly resistant and slightly increasing on inner fringe reefs (mean relative change 18.9%) but vulnerable on outer leeward reefs (mean relative change -34.9%), with *Porites* growth forms, particularly non-branching *Porites* and *Porites rus,* being the dominant contributors of the focal genera assemblages across all reef types. This coral composition shift to *Porites* over the past three decades will most likely result in degraded reef functionality compared to the past, with lower calcification, lower rugosity, loss fish habitat and loss of regional reef associated diversity. Therefore, it is essential to improve local management in order to sustain coral dominated communities through projected global climate change scenarios. Additionally, this thesis can guide the development of coral reef management strategies such as marine protected area design and coral restoration which require ecological context of past and present coral community compositions for effective implementation.

Keywords: *micronesia, acropora, porites, coral, climate change*

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Introduction

Initial studies of coral reefs have focused on identifying the geologic mechanisms through which reef growth and calcification occurred (Goreau 1959, Hopley 1982, Stoddart 1969). Two key environmental factors determining reef growth have been global fluctuations in sea levels overlaid upon antecedent topography and varying wave energy (Done 1982, Kayanne et al. 2002, Kleypas 1997, Munk and Saegent 1948, van Woesik & Done 1997, van Woesik et al. 1995). These processes operating at different temporal and spatial scales have combined to dictate where reef growth existed historically, and where it can now persist (Houk & van Woesik 2010, Done 1982, Loya et al. 2001). Yet, the modern coral assemblages that exist on historical reef structures are dictated by a suite of fine-scale abiotic and biotic factors (Done 1982, Done 1983).

Localized abiotic factors serve as filtering agents to create local assemblages from regional species pools (Cornell & Karlson 1996, DeVantier & Turak 2020, Done 1982, Houk & Starmer 2009, Houk & van Woesik 2010). Some abiotic factors that determine spatial structuring of local coral assemblages are wave energy, light, depth, nutrient inputs, proximity to rivers, and water temperature. Wave energy exerts persistent physical force on reef structures that influence growth form, colony size, recruitment and species composition (Connell et al. 1997, Done & Potts 1992, Grigg 1998, Massel & Done 1993, Jokiel et al. 2004). Water quality parameters such as nutrient levels can influence reef systems in many ways, but primarily through regulating the amount of productivity in an area. Areas where productivity is optimal may lead to increased coral growth and diversity, however, below or above this threshold fewer tolerant species are able to survive. For example, on the Great Barrier Reef (GBR) corals show a distinct diversity gradient with diverse *Acropora* communities far from river mouths and low diversity *Porites* assemblages near river mouths (van Woesik et al. 1999). Excess nutrient input can also fuel growth of macroalgae which in some cases can outcompete corals for space on the reef (Goreau 1971, Sheppard 1982, Lapointe 1997, Rasher and Hay 2010). Other coral composition patterns are influenced by light and depth, which are inherently linked. These gradients are developed through necessity of different coral holobiont photo-productivity (photosymbiosis) and heterotrophic abilities (Edmunds & Leichter 2016, Goreau 1971, Huston 1985). Together, these abiotic factors have been observed to predict modern coral assemblages around numerous islands (Houk & Starmer 2009, Houk and van Woesik 2010).

Biotic interactions on reefs also shape coral communities (Arson and Pretch 1997, Hughes 1994, Pratchett 2010). Coral predation, particularly by the Crown-of-Thorn Starfish, *Acanthaster* spp., can devastate reefs like fire spreading through a forest (Glynn 1974, Randall 1973). Predator starfish have disparate preferences for two dominant coral genera, high for *Acropora* corals and low preference for *Porites* (Birkeland & Lucas 1990, Colgan 1987, Pratchett 2007, Pratchett 2010). It is hypothesized that predator starfish could help maintain high coral diversity when they induce intermediate disturbance frequencies (Connell 1978); cropping fast growing species that would otherwise dominate space and yielding space for slow-growing corals with dense skeletons (Porter 1972, Colgan 1987). However, in recent years, *Acanthaster* outbreaks have increased in frequency (DeVantier & Done 2007) and studies have revealed that outbreaks may be linked with human-induced watershed development, reduction of predators, changing oceanographic patterns due to climate change (Birkeland & Lucas 1990, Houk et al. 2007, Houk et al. 2020a, Kroon et al. 2021, Wooldridge & Brodie 2015).

While abiotic and biotic factors have a long history of investigation, and some are arguably tied or augmented by human stressors, it is now clear that human stressors are exerting a new global filter on coral reefs (Hughes et al 2017, Alvarez-Filip et al. 2013, Loya et al. 2001, Guinotte et al. 2003, Hoegh-Guldberg et al. 2007). The main sources of human stress are pollution, fishing, and their interaction with rising ocean temperatures from climate change (Darling et al. 2019, Hoegh-Guldberg 1999, Houk et al. 2020a, Houk et al. 2020b, Hughes 1994). Understanding where and why some reefs may be resilient has become a priority for many scientists and resource managers. However, baseline data from decades ago before human stressors became dominant are rare, limiting our ability to reveal consistent patterns of change upon which resilience can be assessed.

Many studies have focused generally upon coral cover as a metric of reef ‘health’ or ‘condition’ through time as generalized cover data is widely available (Bruno and Selig 2007, Gardner et al. 2003). However, coral cover alone is inadequate to describe many key processes on reefs that provide ecological functions and ecosystem services. Calcification rates, reef rugosity, complexity, and associated fish habitat vary depending on the coral assemblages and not just cover (Alvarez- Filip 2009, Alvarez-Filip 2013, van Woesik et al. 2015). Thus, it is important to build our understanding of how coral assemblages have shifted through time at both taxonomic and growthform levels, in order to fully appreciate the implications for coral reef ecosystems and to set appropriate management targets (Darling et al. 2013, Pratchett et al. 2010).

Although Indo-pacific reefs are extremely diverse, two coral genera standout as dominant components of modern reefs with contrasting functional roles and life histories: *Acropora* and *Porites* (DeVantier & Turak 20017, Pratchett et al. 2020, Veron 1986, Wallace 1999). *Acropora*

(Oken 1815) have been dominant components of coral reef ecosystems for millennia (Carbone et al. 1994, Wallace 1999). This dominance is attributed to their ability to form large arborescent and branching colonies combined with some of the fastest growth rates of any coral taxon. These characteristics allow them to create an overstory on reefs which make them important functional components of reefs; important to reef calcification, reef complexity, and habitat creation (Alvarez-Filip et al. 2009, Kayanne et al. 2002, Graham et al. 2013). Historically, *Acropora* populations have been viewed as 'competitive' in the sense that they are able to quickly establish new substrates and recover following acute or pulse stress events (Connell et al. 2004). However, *Acropora* are also viewed as a sensitive group due to sensitivity to local stressors, for example, low tolerances to temperature fluctuations, land-based sources of pollution, physical stress(storms); and face high risk from coralivorous pest outbreaks and disease (Done et al. 2007, Madin et al. 2012, Pratchett 2010, West & van Woesik 2001). Looking at future scenarios, *Acropora* are considered by many as potential climate change ‘losers’ due to low thermal tolerance and high mortality rate following bleaching (Loya et al. 2001, van Woesik et al. 2011). If localized stressors continue and the frequency and intensity of climate driven stress events increase, it is thought that *Acropora* populations may decline and become locally extinct into the future (Donner & Carilli 2019, Pratchett et al. 2020). However, in the context of evolution to climate-change stressors, some evidence suggests that *Acropora* may better suited to adapt than many other corals (Guest et al. 2012).

Porites (Link 1807) is another dominant reef forming genus, which are known to form large, dense colonies that can dominate reefs where abiotic conditions are extreme and unfavorable for most other corals (Done 1982, Pichon 2011, Potts 1985). However, *Porites* are slow growing and provide less habitat complexity and reef accretion (Alvarez-Filip et al. 2013, Courtney et al.

2020). For example, in the Maldives *Porites* reefs have 8-times lower carbonate production (1.8 G) than *Acropora* reefs (8.4G), and net annual accretion rates decreased from 4.2mm to -0.4mm following a community composition shift from *Acropora* to *Porites* dominance (Perry and Morgan 2017). *Porites* are considered potential climate change 'winners' due to their high thermal tolerance, deep tissue layer, and resilience to coral bleaching (Cote & Darling 2010, Green et al 2008, Loya et al. 2001). While *Porites* often exhibits relatively stable populations in the face of stressors, thresholds may be passed which they cannot withstand. Any significant loss of this stress-tolerant family would likely have devastating impacts for Pacific Island communities, as they may be some of the last remaining reef building corals given these increasing stressors (van Woesik et al. 2015).

Micronesia, western Pacific Ocean, is an ideal location to study the population dynamics of these two influential coral genera through time. Coral assemblages in Micronesia are diverse, comprising of over 300 species of scleractinian corals on most high islands (Houk et al. 2016, Houk & Starmer 2008, Turak & DeVantier 2005, DeVantier & Turak 2017). Yet, in recent years both local stressors and climate change impacts have been reshaping the modern coral assemblages (Crane et al. 2017, Houk et al. 2012, Houk et al. 2015, Houk et al. 2020a, McLean et al. 2016). In the face of these rapid changes to reef systems, there is an urgent need to review and synthesize quantitative data to extract baselines, albeit already potentially shifted (Pauly 1995), upon which future predictions can be improved. The present study sought to understand the past and present distribution of *Acropora* and *Porites* assemblages in order to help predict what functions reefs have lost and what functions can be expected into the future.

Null Hypotheses:

HO1: The percent cover of *Acropora* and *Porites* does not differ across reef type or geographic sectors in Micronesia during any timepoint. This was rejected if there was significant difference detected from a null model, using a mixed-effects regression modeling that treats geographic sectors as fixed components of variation and islands as random components of variation.

HO2: The growthform-group composition of *Acropora* and *Porites* does not differ across reef type or geographic sectors in Micronesia during any timepoint. This was refuted if a nested, Permutational multivariate analysis of variance (PERMANOVA) shows significant differences in percent contribution of growthforms based upon geography or time period.

H03: There was no relationship between composition of *Acropora* or *Porites* and the change in total coral cover through a Degree Heating Week (DHW, defined below) stress event. This was rejected if there is a strong and significant correlation using a linear regression of genera composition before thermal event to change in total coral cover through a DHW event.

H04: The change of *Acropora* or *Porites* does not vary by geographic sector through a strong (>10) DHW event. This was rejected if there is significant difference detected from a null model, using a mixed-effects regression modeling that treats geographic sectors as fixed components of variation and islands as random components of variation.

HO5: There was no relationship between change of focal genera cover and cumulative DHW stress. This was rejected if there is significant difference from a null model, using a mixed regression model with relative change in focal genera as a dependent variable, cumulative daily

DHW values (>4) as a fixed independent variable, and geographic sectors and islands as random components of variation.

Methods:

Site Description

This study was conducted across four Micronesia islands: Yap, Pohnpei, Chuuk, and Kosrae (Figure 1). These islands have varying degrees of human population, fishing pressure, and watershed development (Houk et al. 2015), along with different exposures to climate-induced ocean warming events (Houk et al. 2020a). In sum, the region has experienced varying levels of acute and chronic disturbance in a spatially and temporally inconsistent manner that have led to changes in coral assemblages through time that are ideal for the present study (McLean et al. 2016, Houk et al. 2015, Houk et al. 2020a). First, this study sought to understand the spatial and temporal trends of *Acropora* and *Porites* by compiling available data from 4 distinct timeframes: (1) 1980s (1986-1987), the oldest known quantitative data collected during two coastal resource inventories for Kosrae and Yap, (2) mid 2000s (2005-2011), an aggregation of early rapid ecological assessments from various programs, and data collected at the start of the Micronesia-wide coral reef monitoring program; (3) mid 2010's (2012-2016) and (4) late 2010s (2018-2020) using the same Micronesia coral reef monitoring program data. These unique historic perspectives were combined across the region to better understand the patterns and potential processes that are driving the dynamics of *Acropora* and *Porites* populations. Last, this study sought to investigate if recent disturbance regimes have led to consistent changes in the distribution of these two prominent genera. For this, exact sites that were repeatedly surveyed in separate years were used to calculate coral change metrics which were directly paired with island level DHW stress indicators.

Rapid Ecological Assessments

Past coral data were derived from historic rapid ecological assessments (REA) collected through the region. Three REAs from Yap 1987 (Coastal Resource Inventory, CRI), Kosrae 1986 (CRI), and Pohnpei 2005 (Turak & Devantier 2005) used a 'DACOR' approach to qualitatively assess the abundance of corals present at a given site. This approach entailed an observer swimming over an area of approximately 5000m² of reef from depths of 1-10 meters, recording species diversity and assigning an estimate of abundance for each species (Dominant, Abundant, Common, Occasional, Rare) (Turak & DeVantier 2005). These DACOR surveys were aligned with current coral quadrat techniques using a method described in future sections. Two additional REAs, Chuuk REA 2008 and Yap REA 2007, were used in this study. Data from these two REAs were collected using a coral quadrat method which matches the present-day Micronesia Challenge Monitoring methodology described below. The only difference being that these surveys used eight quadrats rather than the current Micronesia challenge methodology of 10 quadrats.

Micronesia Coral Reef Monitoring

Since 2009, the study islands have been monitored to guide effective marine resource management and understand recent ecological changes (Houk et al. 2015). Sites were selected to be representative of all major habitats, wave exposures, and management regimes. Survey depth was selected to assess the zone optimal for coral growth; 8-10m on outer reefs and 6-8m on inner reefs. The present study used coral-assemblage data that were surveyed using ten 1-m² quadrats at each site, with quadrats placed at evenly spaced intervals along five (5), 50-m transect lines that defined a site. Within each quadrat, all coral colonies with their center points inside the quadrat boundary are identified to the lowest taxonomic resolution possible, then measured for maximum diameter (x), and for the diameter perpendicular to the maximum (y). Geometric diameters, areas, and coral cover are generated from these measurements. Coral taxonomy identification of each observer for the MC database was verified by Dr. Peter Houk (UOG Marine Lab) for consistency.

Benthic substrate data were collected using approximately $0.5m^2$ meter photo-quadrats of the sessile community at 1-m intervals along five (5), 50 meter transects. Benthic photographs were then processed using the freely available coral point count software CPCE (Kohler & Gill 2006), and substrates under 5 randomly allocated points were evaluated. Benthic categories used for analyses included (i) corals (to genus level or genus plus colony growth form) (ii) turf algae, (iii) macroalgae (iv) encrusting calcareous algae (v) Fleshy coralline algae (vi) sand, and (vii) other invertebrates.

Taxonomy

Corals were typically identified to the species level by each observer during each study year however, analyses will be focused on *Acropora* and *Porites* defined at the genus (i.e., HO1, HO3, HO4, HO5) or growth form level (i.e., HO2). Growth form groupings were defined by major growth forms within each genus: *Acropora* staghorn/arborescent, *Acropora* plate, *Acropora* corymbose/digitate, *Porites* non-branching, *Porites rus* complex, and *Porites* branching (Appendix 1). These groupings allow for a more in depth understanding of potential changes that may be masked at the genus level, while still accounting for any taxonomic biases due to varying observers.

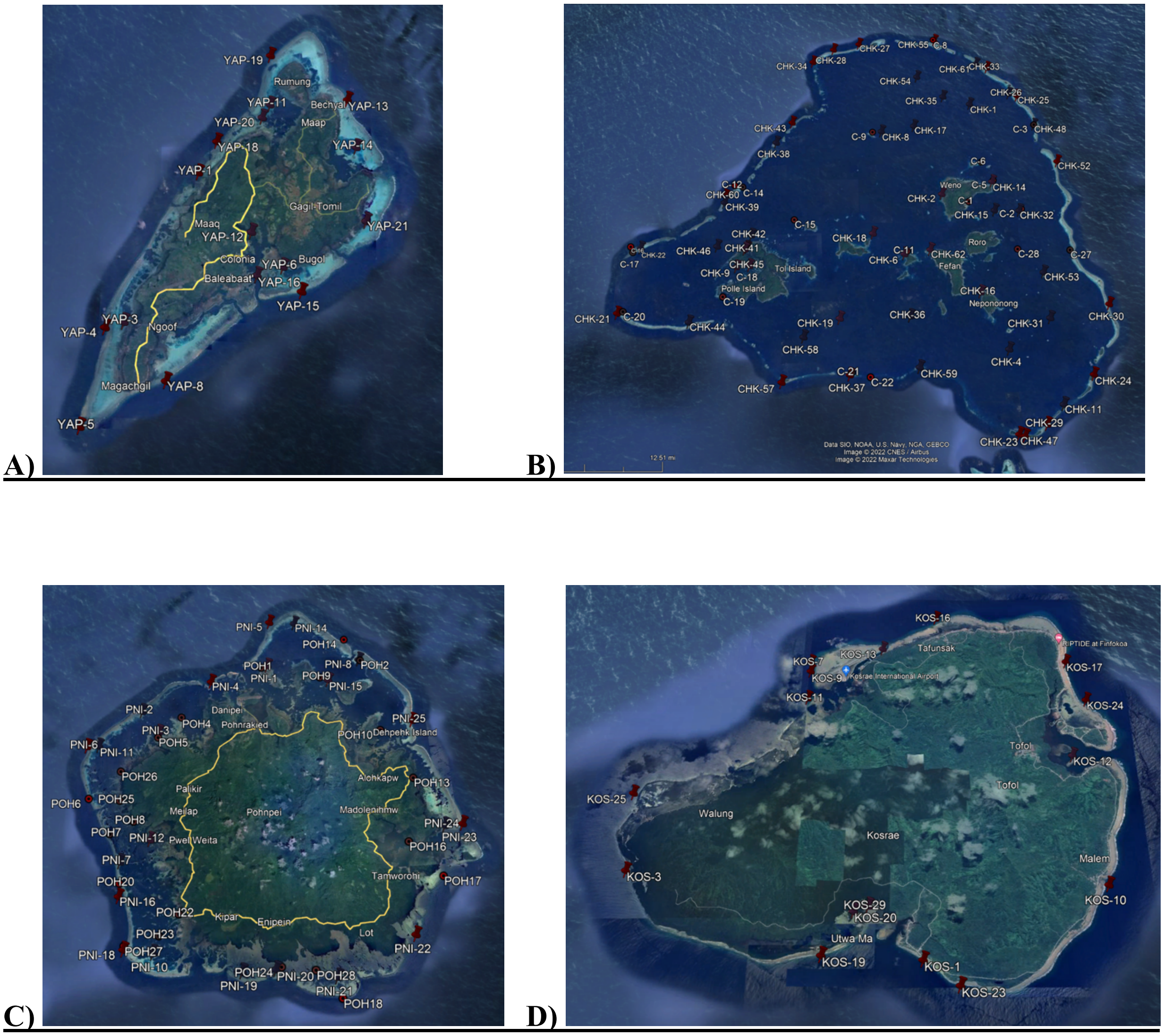


Figure 1. Maps depicting study islands and locations of surveys: Yap (A), Chuuk (B), Pohnpei (C), and Kosrae (D).

Acute Stressors

This study focused on quantifying recent climate-induced bleaching disturbances using degree heating weeks (DHW) that were represented by a fixed factor in our analyses. In contrast, individual islands were treated as random factors to account for any island-level variability that may exist from historical SST and/or chronic stress differences. Degree Heating Weeks represent the degrees above the bleaching threshold calculated over the past 12 weeks. A thermal history of Degree Heating Weeks was created for each island, starting in the year 1985 to the present using NOAA's Coral Reef Watch satellite- derived 5km data (https://coralreefwatch.noaa.gov/product/5km/index.php#data_access). DHW metrics have been used as a proxy to climate-induced warming stress (Donner & Carilli 2019, Kayanne 2016, Mclanahan et al. 2020), and have been shown to covary with the abundance of the coral predator starfish *Acanthaster* at varying time lags (Houk et al. 2020a).

DACOR Surveys

In order to align historical and modern data, historical data from Yap and Kosrae Army Corps Coastal Resource Inventories (1986-1987) were filtered to include hard-bottom reefs only with greater than 10% coral cover. Next, DACOR scores were aligned with present coral estimates following a previous study by McLean et al. (2016). Jenks natural breaks (analogous to K means clustering for a single variable) were used to define five abundance categories from modern data, which match the five DACOR abundance categories used historically. By using the mean value of cover associated with each break one can get a species level estimate for percent cover (D=11.83%, A=4.70%, C=2.40%, O=1.0%, R=0.16%). While this provided a process to give a percent cover value, this data was only used as a dependent variable for spatial analyses. Additionally, regional percent cover values were presented as a general estimate through time but not statistically tested for temporal changes (ie across timepoints). Instead, cover estimates were used to generate values of relative abundances for *Acropora* and *Porites* which were used in temporal comparisons of community structure, described in-depth below.

Data analyses

In order to understand how the spatial distribution of these two genera have changed through time, data were grouped into the previously defined four time periods. Sites were then separated by major reef type and habitat to yield four different reef zones for analytical comparisons: 1) outer windward, 2) outer leeward, 3) inner fringing, and 4) inner patch/back reefs. The percent cover of *Acropora* and *Porit*es was examined at each distinct timepoint for within and between genera differences, using a regional nested linear mixed-effects model with island as a random factor and reef zones or genus as fixed factors. Linear mixed-effects models were performed using the lme4 package in R (Bates et al. 2015).

In order to summarize shifts in the entire *Acropora* and *Porites* assemblages, multivariate approaches were also used. Principle coordinate ordinations (PCO) and permutational multivariate analysis of variance (PERMANOVA) were performed using the proportional contributions values of the total coral assemblage for each of the *Acropora* and *Porites* growthform groups. Then proportional contribution was tested for differences between temporal and spatial components at each defined timepoint (H02). Proportional contribution data were log-transformed and a Bray-Curtis dissimilarity matrix was calculated using the formula $D_{jk} = \sum_{i=1}^{p} \frac{|(Y_{ij} - Y_{ik})|}{(Y_{ij} - Y_{ik})}$, where p is a growthform group; Y_{ij} is the proportional contribution of a functional group at a given site; Y_{jk} is the proportional contribution of a growthform group at a different site. This was visualized in two dimensions using PCO graphs that plot the Bray-Curtis dissimilarity matrix values. These were then further analyzed using multivariate, nested PERMANOVA (HO2). PERMANOVA is a non-parametric test of the null hypothesis that there is no difference in groups through multivariate space. PERMANOVA generates a pseudo-t statistic by using the total sum of squares and within group sum of squares and p-value is calculated by using the t-statistic from the original data and the various permutations of the t-statistic. Last, a SIMPER analysis was performed to observe if there were any changes in the similarity and contribution of growthforms for each reef type through time.

Next, this study aimed to understand how the proportional contribution of *Acropora* or *Porites* before a strong DHW stress (DHW>10) would influence the change of total coral cover through the event (HO3). Benthic data from replicated sites, from three islands that experienced DHW events greater than 10 in 2016-2017 were used: Chuuk, Kosrae, and Pohnpei. A percent cover value of one (1) was added to each site and timepoint to account for particularly low values near zero that would overinflate percentages, similar to Graham et al. 2011 and Ortiz et al. 2018. Then relative change of total coral cover for individual reefs was calculated. Only reefs with greater than 5% composition of either genus were used in analysis. This hypothesis was tested using a regression analysis with log coral composition as the independent variable and log relative change of total coral cover as the dependent variable. Last, regression was weighted by total coral cover at a site before the DHW stress event to give more emphasis to sites with more data and lower standard deviations, and significant results were inspected for residual normality.

Next, this study sought to investigate if any differences in change of *Acropora* or *Porites* existed across reef types, through a strong DHW stress event (defined by DHW>10) (HO4). The same process of calculating relative change (described above) was used to calculate relative change values of focal genera and were analyzed using linear mixed-effects models, that were fit with cover change metrics as the predictor variable, with fixed effects of reef type and island set as a random factor to allow for random y-intercepts.

Last, to quantify how a gradient of DHW stress may influence change of *Acropora* and *Porites* cover (HO5), the same process of calculating relative change was used for all four islands and focal genera change metrics were examined against cumulative DHW stress, now a continuous variable, using a mixed linear regression using the lme4 package in R (Bates et al. 2015). Mixed models set reef type and island as a random factor in order to allow for random variation between both y intercepts and slopes. Dependent variables used were relative change of focal genera, *Acropora* and *Porites,* and cumulative daily DHW stress >4 as a fixed factor. LME models were compared to a null model and if significantly different, the null hypothesis that no significant change has occurred due to DHW stress will be rejected.

Results

Micronesia Degree Heating Week and Acanthaster solaris History

From 1985 to 2016, no Micronesian island experienced a DHW maximum greater than 8 (Figure 2). Only small events were recorded greater than 4; Yap experienced a small thermal event in 1986 (DHW=4.8) and Kosrae in 2013 and 2015 (DHW=6.0; 4.6). In 2016, the ENSO led to unprecedented levels of thermal stress with three islands experiencing events greater than 10 (DHW max: Chuuk =12.6, Kosrae=10.7, and Pohnpei = 13.0). However, Yap experienced no recorded thermal stress events in 2016. In 2017 Chuuk, Pohnpei, and Yap experienced events greater than 8 (DHW max=11.4, 8.7, 8.6) while Kosrae DHW subsided to slightly greater than 4 (DHW max= 4.1). From 2018 to 2020 no thermal events were recorded in the region. In sum, peak thermal stress was observed across all study islands between 2015 and 2017, but the intensity varied.

While quantifying Crown of Thorn Starfish (COTS, *Acanthaster solaris*) outbreak events is challenging, there have been a few notable events since 2000. Chuuk had the greatest frequency of known events, with potentially 3 outbreak events (2008, 2012, 2016). Pohnpei Yap, and Kosrae each had potentially two outbreak events (Pohnpei: 2009, 2016; Yap: 2010, 2015: Kosrae 2013,2017). In sum, all island had been affected to some extent by these predatory starfish since 2000.

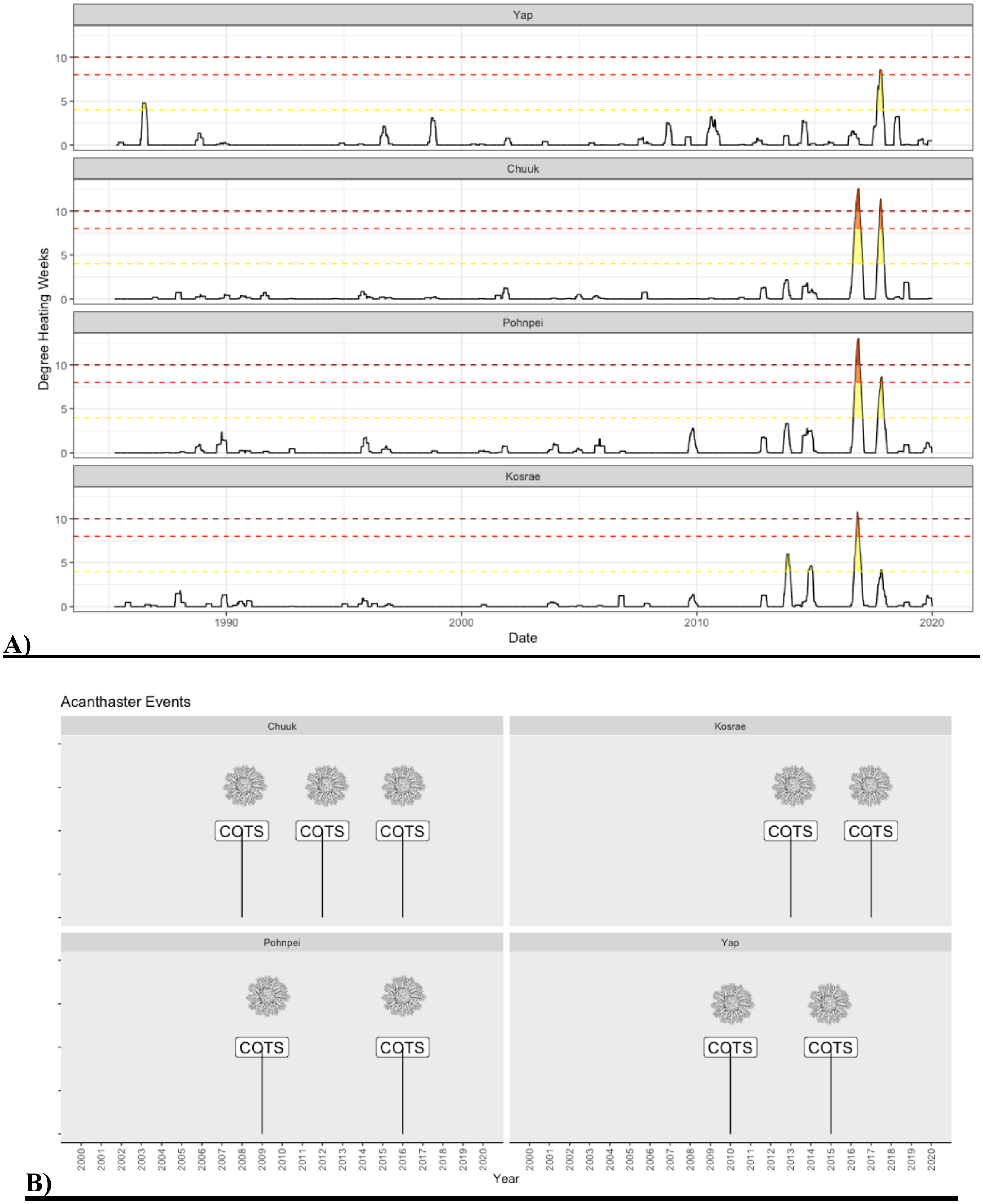


Figure 2. Shows temporal trends of A) Degree Heating Week values and B) known notable *Acanthaster* events for each Micronesian island in this study.

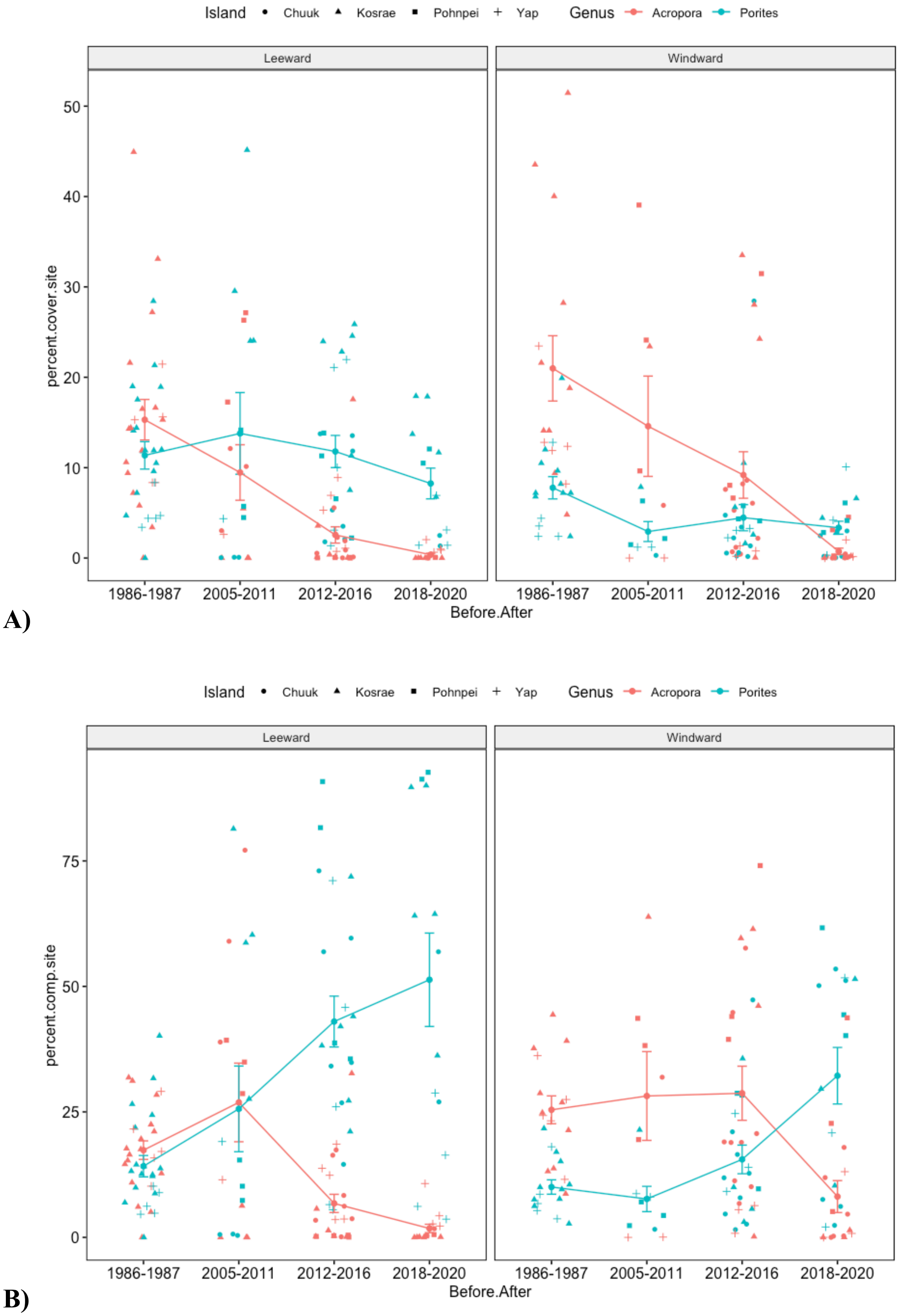
Genera Temporal and Spatial trends on Outer Reefs

Acropora

Both windward (W) and leeward (L) reefs across Micronesia had relatively high cover (mean W=21.0±3.6, L=15.3±2.2) and proportional contribution (mean W=25.4±2.8, L=17.4±1.8) of *Acropora* in the mid-1980's (Figure 3). At this time period there was no significant difference in cover of *Acropora* between windward and leeward outer reefs (χ^2:0.9, P>0.05, Δ AIC: 1.1). By the mid-2000's, *Acropora* cover declined on both island-sides (mean W=14.6±5.5, L=9.5±3.03) but the proportional contribution slightly increased (mean W=28.2±8.8, L=26.9±7.8). Despite the loss in absolute cover of *Acropora*, there was still no significant difference in *Acropora* cover between island sides (χ^2:0.7, P>0.05, Δ AIC: 1.3). *Acropora* cover continued to decline into the 2010's (2012-2016), however the decline was greatest on the leeward with only minimal declines on the windward (mean W=9.2±2.6, L=2.6±0.9). Proportional contribution showed a similar trend of decreasing *Acropora* on the leeward and increasing on the windward (mean W=28.7±5.3, L=6.8±1.8). LME models revealed that there was a significant difference of *Acropora* cover between island-sides with windward reefs supporting two times more *Acropora* cover than leeward reefs (LME, P<0.01, Estimate: 2.0±0.6) (null model comparison, χ^2:7.8, P<0.05, Δ AIC: 5.8). However, during the most recent time period (2018-2020) following the major ENSO driven DHW stress, windward reefs suffered their greatest loss of *Acropora*, with both island-sides now supporting low cover (mean W=0.7±0.4, L=0.4±0.2) and relative contribution (mean W=8.1±3.2, L=1.8±0.8). Due to this decline, LME model revealed no significant difference in *Acropora* between island-sides (null model comparison, χ^2:0.9, P>0.05, Δ AIC: 1.1).

Porites

In the mid-1980’s, *Porites* had relatively low cover on outer reefs (mean W=7.8±1.2, L=11.4 ±1.5) and composition (mean W=10.0±2.2, L=14.2±2.1) on both island-sides. Spatial analysis revealed no significant difference in cover of *Porites* between island-side at this timepoint (null model comparison, χ^2:1.6, $P>0.05$, Δ AIC:0.4). In the late 2000s, *Porites* had a slight decrease in cover and relative composition on the windward and increase in cover and relative composition on the leeward (W=2.9±1.1, L=13.8 ±4.5; W=7.6±8.5, L=25.6±8.5). LME models of this time period revealed a significant difference between island sides ($P<0.05$, Estimate: -1.1±0.4), with less *Porites* on the windward than the leeward (null model comparison, χ^2:6.6, $P<0.05$, Δ AIC: 4.6). In the mid 2010s, *Porites* cover increased on both island sides in cover and relative composition (W=4.5±1.8, L=11.8±1.8; W=15.5±2.9, L=43.0±5.1) with a significant difference between island-side, with significantly lower *Porites* cover on the windward then leeward ($P<.001$, Estimate: -1.3±0.4) (null model comparison, χ^2:11.5, $P<0.001$, Δ AIC: 9.52). Most recently (2018-2020), the windward and leeward slightly decreased in cover (W=3.4±0.7, L=8.2±1.7) while the relative contribution continued to increase (W=32.2±5.6, L=51.3±9.3), albeit with significantly lower cover of *Porites* on the windward than leeward ($P<0.05$, Estimate: -0.4±0.3) (null model comparison, χ^2:6.0, $P<0.05$, Δ AIC: 4.0).



<u>Figure 3.</u> Temporal trends in A) cover and B) composition of focal genera on outer reefs by island-side.

Acropora versus Porites

In the late 1980s, there was a significant difference between the cover of *Acropora* versus *Porites* on windward outer reefs with less cover of *Porites* than cover of *Acropora* (LME, $P<0.001$, Estimate: -1.0±0.27) (null model comparison, χ^2:11.9, $P<0.001$, Δ AIC: 10.0). No significant difference was detected between *Acropora* versus *Porites* on the leeward during this time period (null model comparison, χ^2:1.6, $P>0.05$, Δ AIC: 0.4). In the late 2000s, there was a significant difference between *Acropora* versus *Porites* on the windward with significantly less *Porites* than *Acropora* ($P<0.05$, Estimate: -1.6±0.7) (null model comparison, χ^2:4.2, $P<0.05$, Δ AIC: 2.3). In contrast, there was no significant difference between *Acropora* versus *Porites* on the leeward during this time period (null model comparison, χ^2:0.4, $P>0.05$, Δ AIC: 1.6). In the mid 2010s, there was no significant difference between *Acropora* versus *Porites* cover on windward reefs (null model comparison, χ^2:2.2, $P>0.05$, Δ AIC: 0.2). However, there was a significant difference between *Acropora* versus *Porites* on the leeward during this time period with significantly more *Porites* than *Acropora* on the leeward (LME, $P<0.001$, Estimate:2.0±0.7) (null model comparison, χ^2:25.3, $P<0.001$, Δ AIC: 23.3). In the late 2010s, there was a significant difference in cover between *Acropora* versus *Porites* on both island-sides with significantly more *Porites* on the windward (LME, $P<0.001$, Estimate:7.1±5) and leeward (LME, $P<0.001$, Estimate:2.2±0.3) (null model comparison, windward χ^2:14.3, $P<0.001$, Δ AIC: 12.3; leeward χ^2:26.2, $P<0.001$, Δ AIC: 25.23).

Genera Temporal and Spatial trends on Inner and Patch/back reefs

Acropora

In the late 1980s inner reefs coral assemblages had moderate cover and composition of *Acropora* (7.2±2.4,12.2±4.0 cover and composition respectively). By the late 2000s *Acropora* cover had declined by almost half (3.9±1.4, 11.1±3.6). *Acropora* continued to decline into the mid 2010s, reaching below 1% cover (0.9±0.3, 2.9±01.0). In the late 2010s, *Acropora* slightly decreased in cover and composition again (0.2±0.1; 0.6±0.3). It should be noted that in this last timepoint, no coral quadrat data were available for Pohnpei inner reefs and thus it was not included or represented in the regional means for this timepoint.

No data were available for patch/back reefs for the 1980s and the following trends are only for the islands of Pohnpei and Chuuk which have sufficient data from patch/back reefs. In the earliest timepoint of the late 2000s, patch/back reefs already had low *Acropora* cover (4.3±1.7,17.9±7.5). By the mid 2010s, *Acropora* remained relatively stable (3.7±2.7, 15.8±5.0). In the most recent time period (2018-2020), *Acropora* decreased reaching extremely low cover and composition values (*Acropora* 0.3±0.1, 2.8±0.9).

In the late 2000s there were no significant differences of *Acropora* cover between inner vs patch/back reefs (null model comparison, χ^2:1.1, P>0.05, Δ AIC: 0.85). However, in the mid 2010s, patch/back reefs did have significantly more *Acropora* cover than inner reefs (P<0.05, Estimate:1.7±0.7) (null model comparison, χ^2:5.3, P<0.05, Δ AIC: 3.3). In late 2010's there was still a significant difference between *Acropora* cover on inner vs patch/back reefs (P<0.01, Estimate:0.9±0.3), (null model comparison, χ^2:7.1, P<0.001, Δ AIC: 5.07).

Porites

In the late 1980s, coral assemblages on inner reefs were already predominantly composed of *Porites* (13.3±2.6, 23.6±4.9, cover and composition respectively). By the late 2000s *Porites* increased in both cover and composition (18.5±2.8, 54.0±6.0). This trend continued into the mid 2010s as both cover and composition of *Porites* increased (28.7±3.3, 85.4±3.4). In the late 2010s, *Porites* slightly decreased in cover and composition (*Porites:* 17.6±2.2; 82.8±5.0). Again, it should be noted that in this last timepoint, no coral quadrat data were available for Pohnpei inner reefs and thus it was not included or represented in the regional means for the 2018-2020 timepoint.

In the earliest timepoint of the late 2000s, patch/back reefs were already dominated by *Porites* (16.7±2.5, 65.4±9.3). By the mid 2010s, *Porites* increased in cover and slightly decreased in relative composition (21.3±2.6,63.2±5.7). In the late 2010s, *Porites* decreased in cover and increased in composition (8.2±1.7, 67.5±5.2).

In the late 2000s there was no significant difference in *Porites* cover between inner and patch/back (null model comparison, χ^2:0.9, $P>0.05$, Δ AIC: 1.1). In the mid 2010s, there was a significant difference between *Porites* cover between inner and patch/back reefs, with significantly less Porites on patch/back reefs compared to inner reefs (LME, $P<0.01$, Estimate: -2.2±0.7) (χ^2:8.0, $P<0.01$, Δ AIC:6.0). In the late 2010s there was a significant different between reef types, with significantly less *Porites* on patch/back reefs than on inner reefs (LME, $P<0.05$, Estimate: -1.4±0.5) (null model comparison, χ^2:6.3, $P<0.05$, Δ AIC: 4.32)

Acropora* versus *Porites

There was no significant difference in *Porites* versus *Acropora* cover on inner reefs in the early 1980s (null model comparison, χ^2:3.0, P>0.05, P=0.08, Δ AIC: 1.0). There was significantly more *Porites* versus *Acropora* on inner reefs in late 2000s, mid 2010s and late 2010s (LME, P<0.001, 0.001, 0.001, 0.001; Estimates: 5.4±0.8, 9.5±0.4, 9.4±0.4; respectively) (null model comparison, χ^2: 37.5, 35.5, 89.2; P<0.001,0.001,0.001; Δ AIC: 35.5, 33.5, 87.2).

There was significantly more *Porites* than *Acropora* on patch/back reefs at all study timepoints; in the late 2000s, mid 2010s and late 2010s (P<0.001,0.001,0.001; Estimates: 5.2±1.1, 5.6±0.8,7.1±0.5 respectively), (null model comparison, χ^2:14.8, 35.5, 76.8; P<0.001, 0.001, 0.001; Δ AIC: 12.8, 69.8, 74.8 respectively).

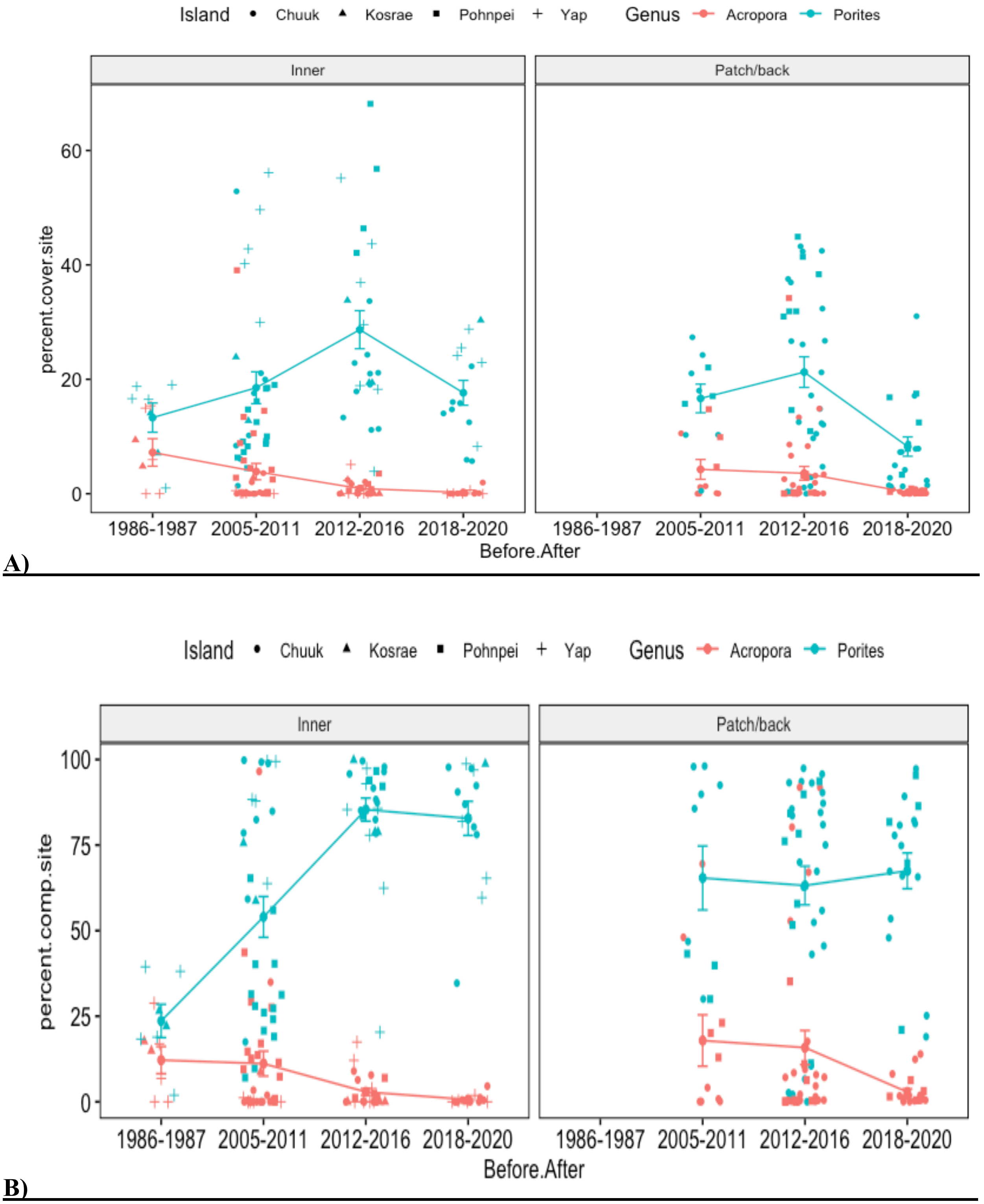


Figure 4. Trends of cover (A) and composition (B) of focal genera on inner and patch/back reefs. Note that lines between timepoints do not represent constant rate of change and that number of years between time periods vary.

Growthform Composition

Principle components ordination (PCO) of *Acropora* and *Porites* growthforms revealed that 55.2% of the variation between Micronesian outer reefs was explained by the first axis (PCO1) (Figure 5). An interesting pattern emerged, where the vectors associated with *Porites* and *Acropora* growthforms were negative and positive along the x-axis of the PCO, respectively. PCO2 explained an additional 22.6% of the variation between Micronesian reefs with *Porites* non-branching (negative), *Porites rus* (positive), and *Porites* branching (positive) growthforms most influential. *Acropora* growthforms were less influential to PCO2 with *Acropora* digitate/corymbose (positive) depicted in the opposite direction of *Acropora* staghorn/arborescent and *Acropora* plate (positive).

These temporal investigations confirmed the above trends showing Micronesian reefs had a large proportional contribution of *Acropora* growth forms on both windward and leeward reefs in the late 1980s. This is depicted through high PCO1 scores (windward: 20.16, leeward: 15.13, Figure 5). A nested regional PERMANOVA during this time period showed no significant difference in growthform composition between island side at this time period (P>.05, t=0.7). In support, simper analyses showing which coral growth forms were most influential to the PCO highlighted *Acropora* plate, *Porites* non-branching, *Acropora* staghorn/arborescent as most influential for windward reefs (Simper contribution values, 29.26%; 28.72%; 25.76%, respectively), and *Acropora* staghorn/arborescent, *Porites* non-branching, *Acropora* plate for leeward reefs (Simper contribution values, 28.15%; 25.72%; 20.49%, respectively) (Figure 6).

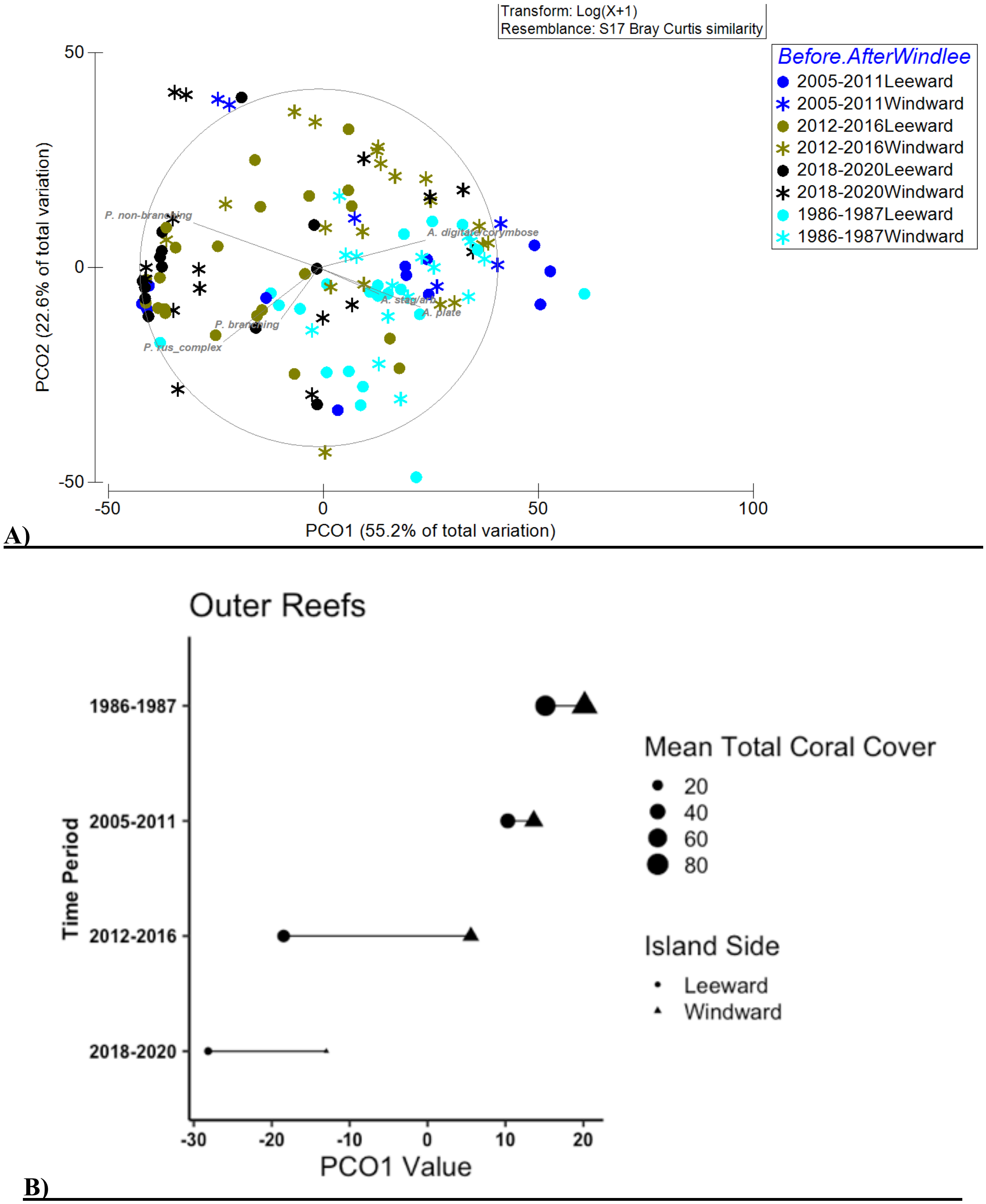


Figure 5. (A) PCO of *Acropora* and *Porites* growthforms based upon proportional contribution data aggregated to the site level (i.e., each symbol represents a site), with primary vectors displayed in grey. (B) Summary of PCO1 trends for leeward and windward reefs at each timepoint to illustrate temporal trends. Dots represent location of regional centroid for windward and leeward reefs along PCO1 at each timepoint.

In the late 2000's, Micronesian outer reefs still had large proportional contributions of *Acropora* growthforms on both island sides demonstrated by positive PCO scores (windward:13.64, leeward: 10.30, Figure 5B). A nested regional PERMANOVA during this time period showed no significant difference in *Acropora* and *Porites* growthform contribution between island side at this time period (PERMANOVA, $P>0.05$, $t=1.1$). Yet, Simper analyses began to reveal some distinction between windward and leeward reefs. *Porites* non-branching, *Acropora* digitate/corymbose, and *Acropora* staghorn/arborescent were most influential on the windward (Simper contribution values, 55.76%, 18.28%, 15.06% respectively), while *Acropora* digitate/corymbose, *Porites* non-branching, *Porites* rus complex were most influential on the leeward (Simper contribution values, 25.56%, 24.4%, 18.22% respectively) (Figure 6). Last, inter-timeframe comparisons of coral assemblages of island side to itself showed no significant differences between the late 1980's and late 2000s times for (PERMANOVA, $P>0.05$, windward $t=0.6$, leeward $t=0.8$).

In the mid 2010s, coral communities on the windward remained relatively high in *Acropora* growthform contribution (PCO1=5.6) while leeward reefs were more dominated by *Porites* (PCO1= -18.5) (Figure 5). At this timepoint a nested PERMANOVA showed that windward and leeward reefs communities were significantly different (PERMANOVA, $P<0.05$, $t=1.7$). Non-branching *Porites* was the largest contributor on both windward and leeward reefs (Simper contribution values, 39.3%,49.8%). The largest *Acropora* growthform contributor was *Acropora* corymbose/digitate on the windward and leeward (Simper contribution values, 32.7%,12.0%). The windward still had a large Simper contribution values of *Acropora* staghorn/arborescents during this time period (15.4%) while on the leeward they continued to decline (2.2%) The *Acropora/Porites* community on the leeward of this time period was significantly different than its community of 1986-1987 (PERMANOVA, $P<0.05$, $t=2.4$) however not 2005-2011 (PERMANOVA, $P>0.05$, $t=1.5$). The windward community showed little shift in community structure, being not significantly different from itself during any previous time periods (PERMANOVA, $P>0.05$, $t=1.3$, $t=0.7$).

In the late 2010s leeward reefs continued to transition to communities more heavily dominated by *Porites* (PCO1= -28.2). Windward reefs followed a similar shift but to a lesser extent (PCO1= -13.0). The most common coral growthform remained *Porites* non-branching reaching over 50% on both windward and leeward (Simper contribution values, 58.0%,53.2%) Due to this shift in the same direction, island-sides were no longer significantly different (PERMANOVA, $P>.05$, $t=0.8$). *Porites rus* complex rose greatly in contribution and became the second greatest contributor on both windward and leeward (Simper contribution values, 23.1%, 39.7%). On the leeward the last major *Acropora* growthform was digitate/corymbose and the staghorn/arborescents and plates were nearly absent (L=6.0, 0.0, 0.4 respectively). However, the windward was able to maintain slightly higher contribution of all *Acropora* growthforms (Simper contribution values, digitate/corymbose=11.2, plate=5.4%, staghorn/arborescent =2.0%). The leeward communities were only significantly different when comparing the 2012-2016 and 2018-2020, to the 1986-1986 community (PERMANOVA, $P<0.5$, $P=0.5$, $t=2.4$, 2.5 respectively). While the windward was only significantly different than itself when comparing the 2018-2020 community to the 1986-1987 community (PERMANOVA, $P<0.05$, $t=2.1$).

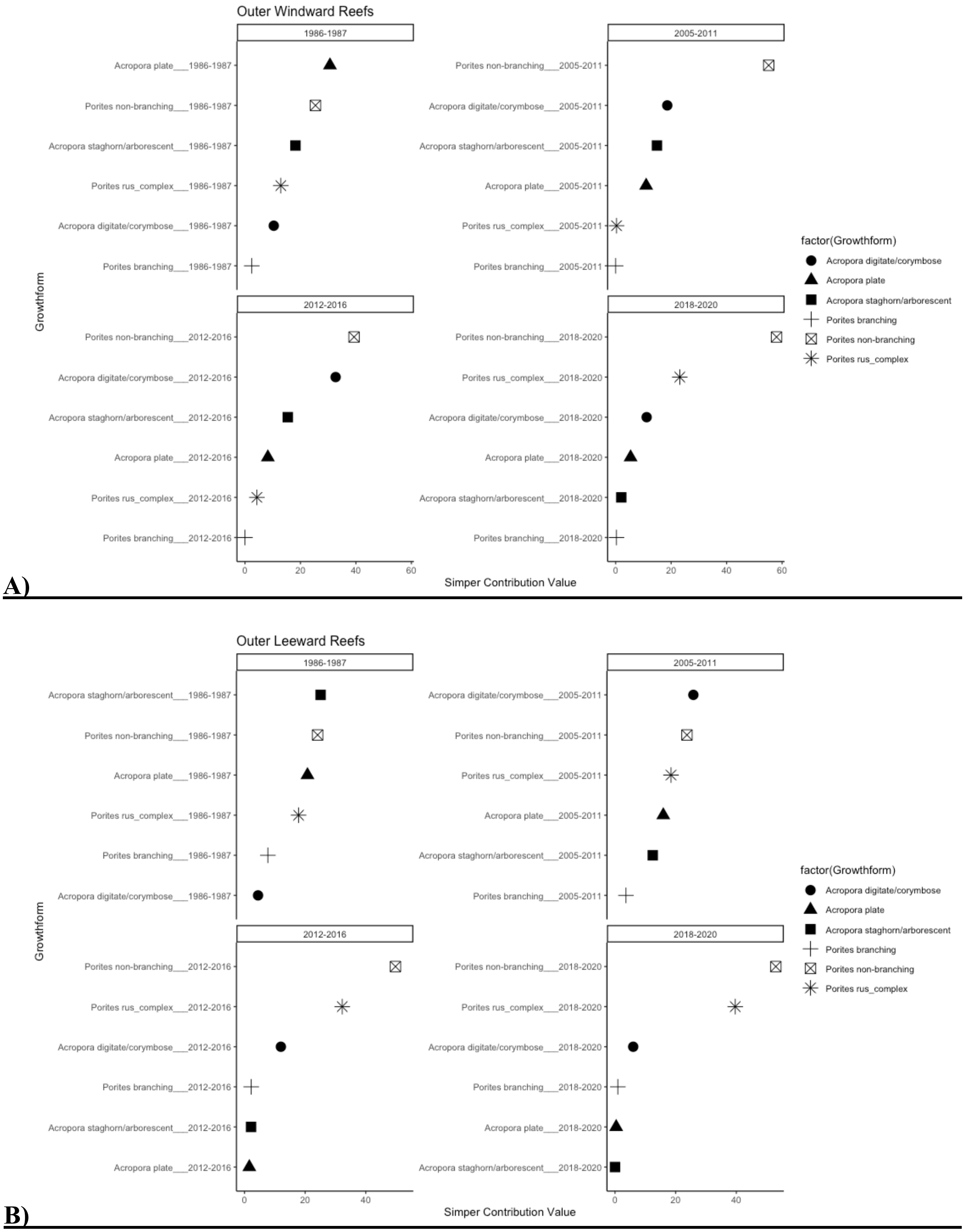


Figure 6. Simper contribution values of outer reefs showing major contributors of A) windward and B) leeward for each time period.

Principle components ordination (PCO) of *Acropora* and *Porites* growthforms revealed that 42% of the variation on Micronesian inner and patch/back reefs was explained by the first axis (PCO1) and 38.6% of the variation was explained along axis 2 (PCO2) (Figure 7). With *Acropora* growthforms and *Porites* branching positive along and *Porites* non-branching and *Porites rus* complex negative along PCO1. *Porites* branching and *Porites rus* were positive along and *Acropora* growthforms and *Porites* non-branching negative along PCO2. There was no significant difference between inner and patch/back reefs for any time period (2005-2011, 2012-2016, 2018-2020, PERMANOVA, P>0.05, t=0.7, 0.9, 1.2 respectively) and no significant difference within reef type (Inner, 1980s & 2005-2011, 1980s & 2012-2016, 1980s & 2016-2018, PERMANOVA, P>0.05, t=1.5, 2.0, 1.7 respectively; Patch/back, 2005-2011 & 2012-2016, 2005-2011 & 2016-2018, PERMANOVA, P>0.05, t=0.5, 1.0 respectively). No significance between or within reef types through time was most likely due to the historic and consistent contribution of all *Porites* growth forms in these areas. However, further analyses were conducted to see if there were changes in growthform contribution and relative rank.

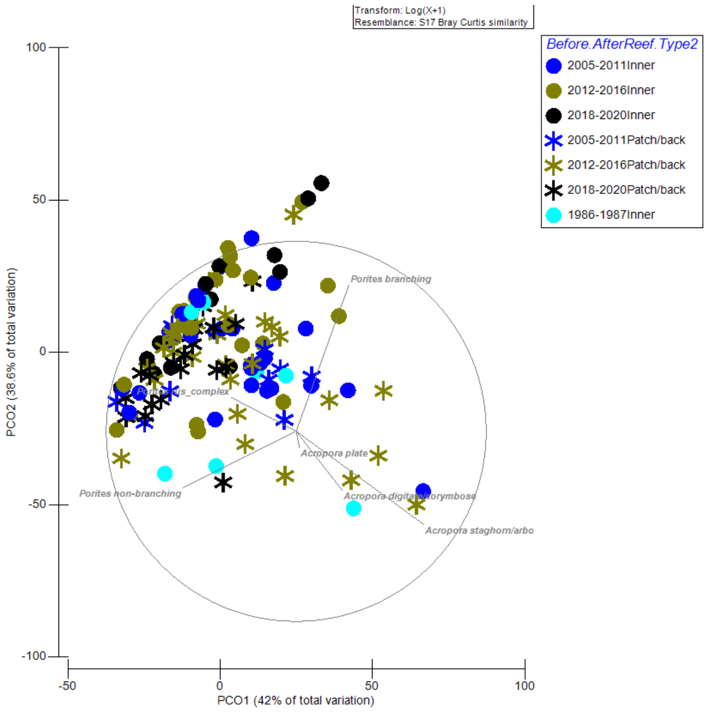


Figure 7. Principal component analysis of inner and patch/back reefs with primary vectors displayed in grey.

Since the 1980's it appears that inner reefs have been dominated by *Porites* growth forms (Figure 8), particularly *Porites* non-branching and *Porites rus* (Simper contribution values, 48.3%, 16.2%). Yet, many *Acropora* growthforms had notable contributions and especially *Acropora* staghorn/arborescent (12.8%). In the late 2000s *Porites* growthforms remained dominant however the most common became *Porites* branching (Simper contribution value, 32.0%). Simper contribution of *Acropora* growthforms did not change rank but did slightly decrease in contribution. In the mid 2010s, *Porites* growthforms remained dominant however the most common became *Porites rus* complex (Simper contribution value, 42.5%). Simper contribution of *Acropora* growthforms did not change in rank however, with Acropora staghorn/arborescents now at 3.5%. In 2018-2020 *Porites* growthforms stayed consistently dominant with *Porites* branching now the most dominant growthform (Simper contribution values, 43.5%). A change was also observed in the *Acropora* growthforms, with a disappearance of virtually all *Acropora* staghorn/arborescents (Simper contribution value, 0.37%).

In the late 2000's *Porites* was the dominant genus on patch/back reefs with *Porites rus* complex being the greatest contributor across sites (45.5%) (Figure 9). Across years the rank of *Porites* growthforms did not change and the contribution only varied slightly. The largest changes were seen in *Acropora* growth forms. *Acropora* staghorn/arborescent was historically the most dominant growth form within the genus (10%), however this continued to slightly decrease from the late 2000s to mid 2010s. In the most recent time period of the late 2010s, *Acropora* staghorn/arborescent declined greatly (1.7%), and the main growth form present across sites became *Acropora* digitate/corymbose (3.9%). The largest contributors remained *Porites rus* (48.2%) and *Porites* non-branching (11.4%) and to a lesser extent the more complex growthform *Porites* branching (11.42%).

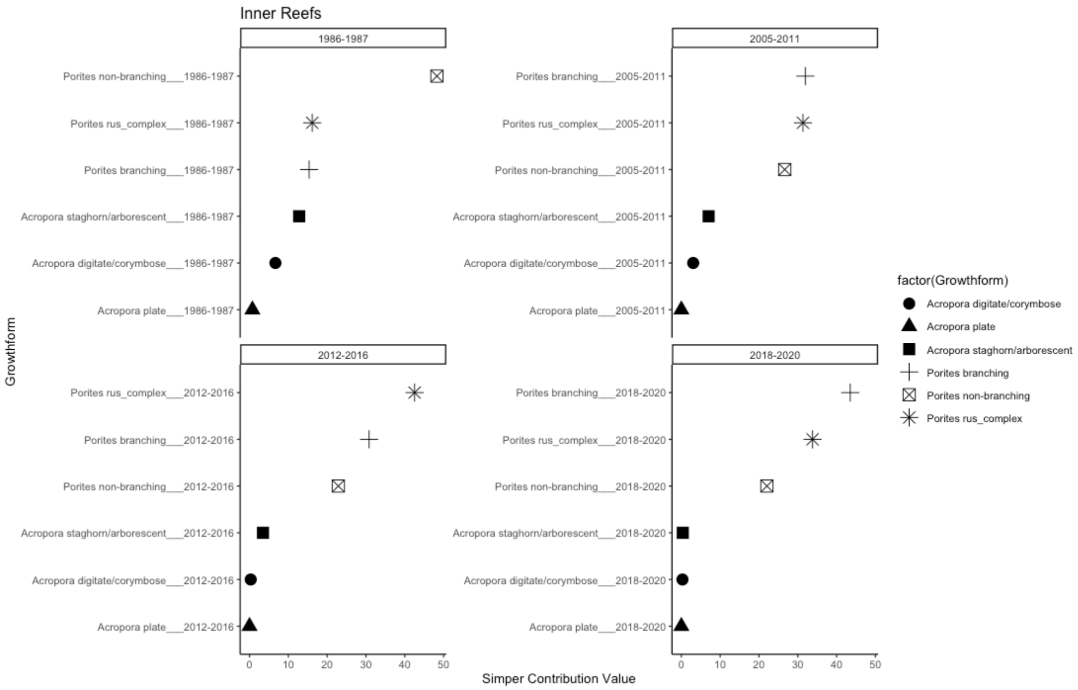


Figure 8. Simper contribution values of inner reefs showing major contributors for each time period.

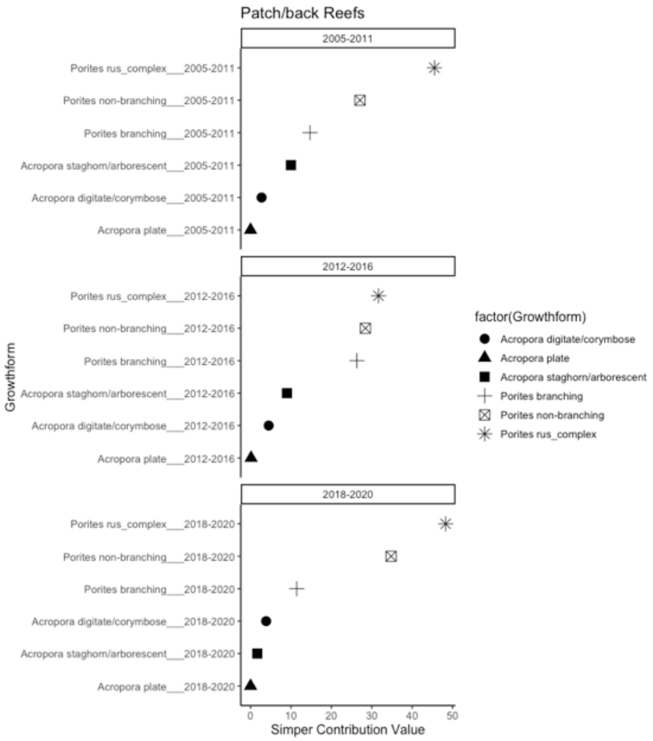


Figure 9. Simper contribution values of patch/back reefs showing major contributors for each time period.

Genera Contribution Through DHW Events

Reefs with higher contributions of *Acropora* were more susceptible to changes in total coral cover through a strong DHW stress event. There was a strong negative relationship between change in coral cover and contribution of *Acropora* ($p<0.001$, adj $R^2=-0.41$, Slope=-3, regression weighted by total percent coral cover before DHW event to reduce inflation of low coral cover reefs) (Figure 10 A). In contrast, reefs with higher contribution of *Porites* were shown to be more resistant to change in total coral cover through a strong DHW stress event. A weighted linear regression of the percent contribution of *Porites* before DHW disturbance event (>10) and change in total coral cover through the event showed a strong positive relationship ($p<.001$, adj $R^2=0.44$, Slope=3.4) (Figure 10 B).

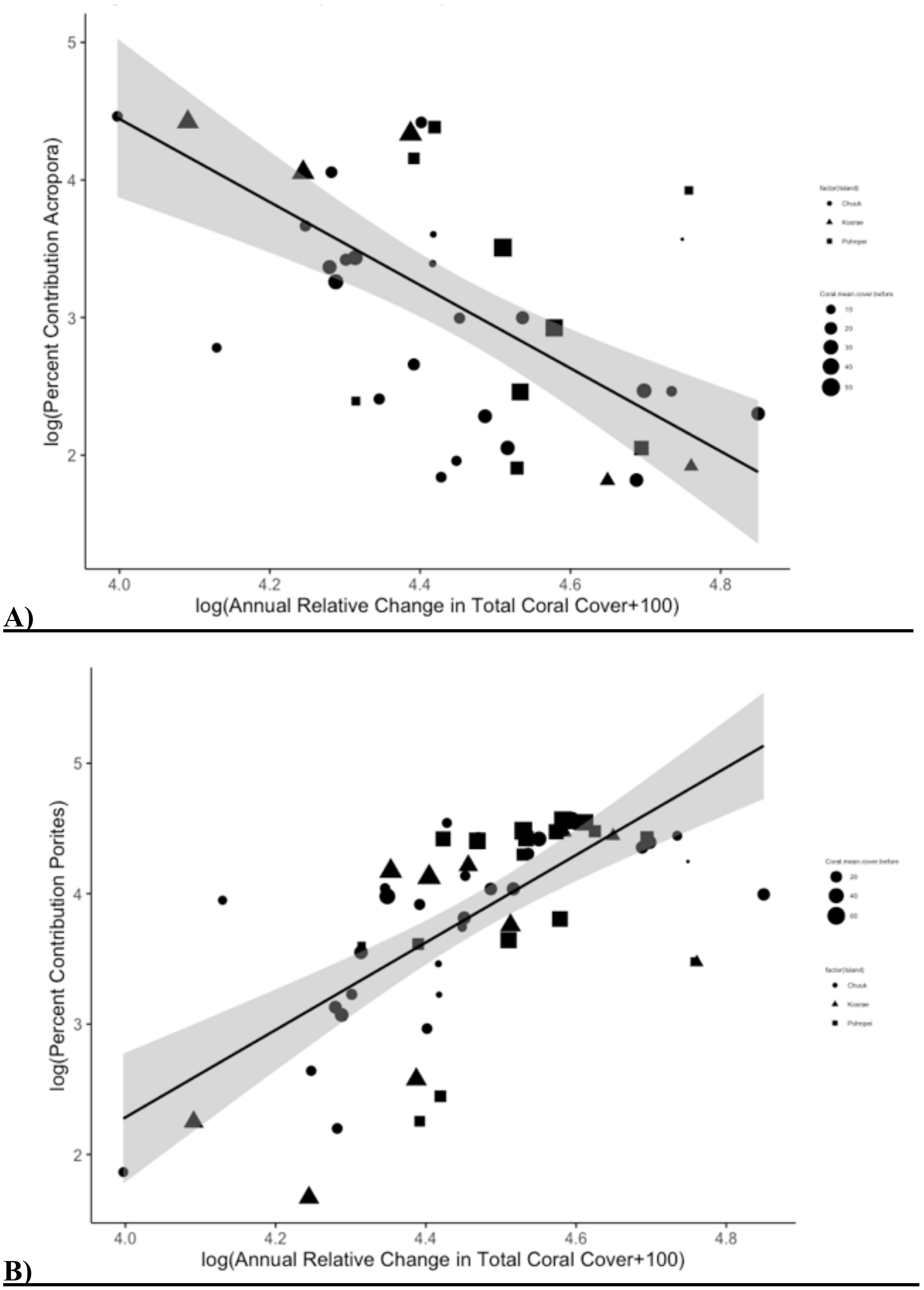
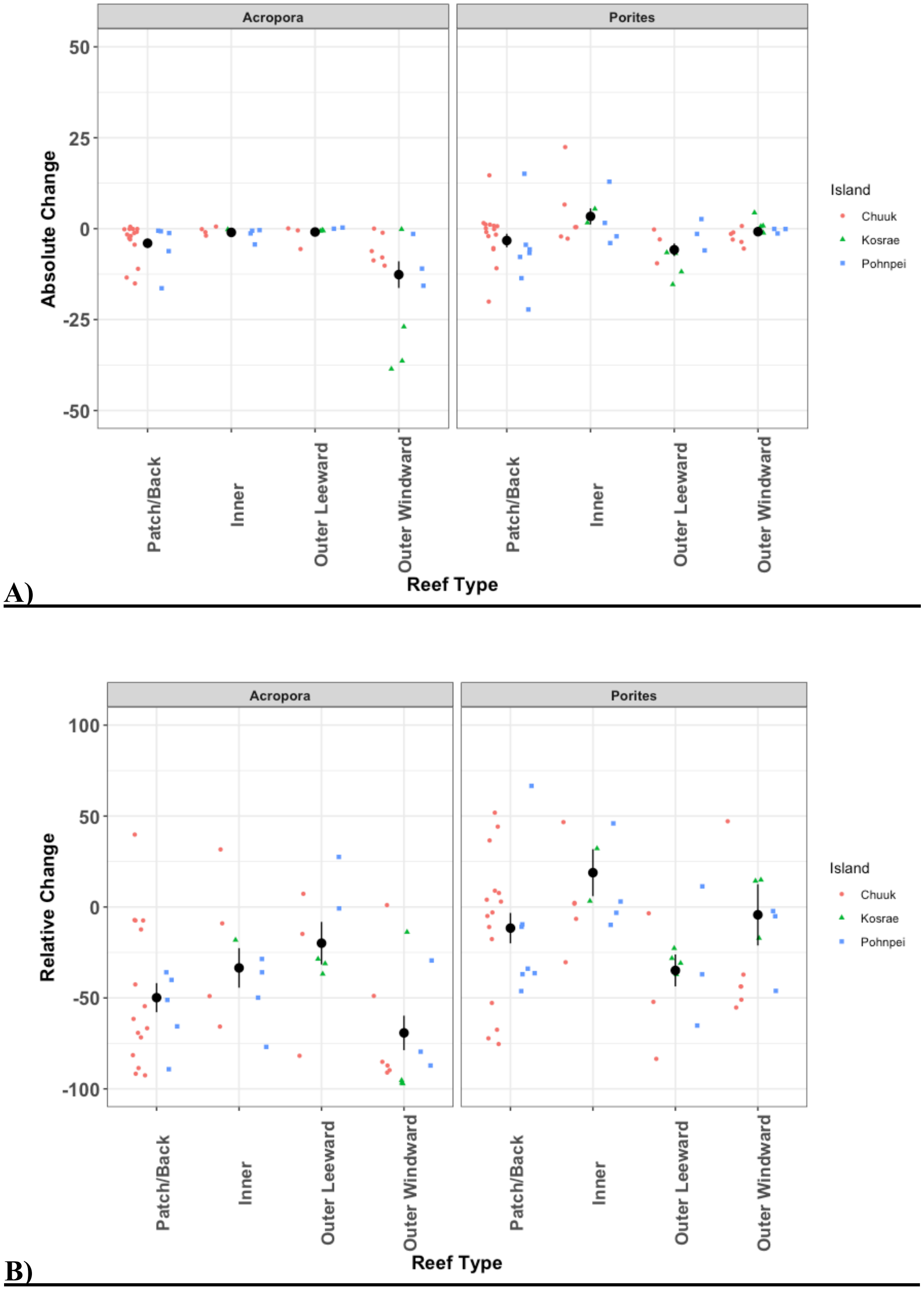


Figure 10. Linear regression between the percent contribution of *Acropora* (A) and *Porites* (B) before the DHW disturbance event in 2016-2017 versus relative change in total coral cover through the event. Note graphic depicts, the x axis with transformed values and a constant of 100 added, thus, any value less than 4.6 were negative change values (ie losses) in total coral cover while any values greater than 4.6 were a positive change values (ie increases) in total coral cover.

Change through DHW event greater than 10

On reefs that experienced a degree heating event greater than 10, a linear mixed effects model (LME) showed that *Acropora* and *Porites* cover declined inconsistently across the study region based upon reef type (Figure 11, Table 1). Among outer reefs, the greatest *Acropora* loss occurred on windward reefs (-12.6±3.7, -69.2±9.5, absolute change (A.C.) and relative change (R.C.) respectively, Figure 11). Among inner reefs, the patch/back reefs were most impacted (-4.0±1.2, -49.8±8.0, A.C. and R.C. respectively). *Acropora* was least impacted on outer leeward reefs, with lowest absolute change and relative change (-0.9±0.7, -19.9±11.7, A.C. and R.C. respectively) and slightly on inner reefs (-1.0±0.5, -33.5±10, A.C. and R.C. respectively). Through the same DHW events, *Porites* showed slight increases on inner reefs (3.4±2.2, 18.9±13.0, A.C. and R.C., Figure 11, Table 1). *Porites* cover changed relatively little on outer windward reefs (-0.8±0.7, -4.2±16.9, A.C. and R.C. respectively). In contrast, *Porites* had largest declines, being most susceptible on outer leeward reefs (-5.8±1.7, -34.9±8.8, A.C. and R.C. respectively) and patch/back reefs to a lesser extent (-3.3±1.9, -11.6±8.3, A.C. and R.C. respectively).



<u>Figure 11.</u> The absolute (A) and relative (B) change for all reef types through a DHW event greater than 10.

	Acropora.absolute.change.log.constant					**Acropora.percent.change.log.constant**					**Porites.absolute.change.log.contant**					**Porites.percent.change.log.constant**				
Predictors	*Estimates*	*std. Error*	*CI*	*p*	*df*	*Estimates*	*std. Error*	*CI*	*p*	*df*	*Estimates*	*std. Error*	*CI*	*p*	*df*	*Estimates*	*std. Error*	*CI*	*p*	*df*
(Intercept)	3.89	0.03	3.83 – 3.95	**<0.001**	44.00	4.47	0.05	4.37 – 4.58	**<0.001**	44.00	3.93	0.01	3.91 – 3.96	**<0.001**	51.00	4.66	0.05	4.57 – 4.76	**<0.001**	51.00
Reef Type 2 [Outer Leeward]	0.02	0.03	-0.05 – 0.09	0.554	44.00	0.05	0.08	-0.10 – 0.21	0.488	44.00	-0.07	0.02	-0.12 – -0.03	**0.001**	51.00	-0.21	0.07	-0.35 – -0.07	**0.004**	51.00
Reef Type 2 [Outer Windward]	-0.08	0.03	-0.14 – -0.03	**0.006**	44.00	-0.16	0.07	-0.30 – -0.02	**0.028**	44.00	-0.03	0.02	-0.07 – 0.01	0.195	51.00	-0.07	0.06	-0.20 – 0.06	0.311	51.00
Reef Type 2 [Patch/Back]	-0.03	0.03	-0.08 – 0.02	0.273	44.00	-0.07	0.06	-0.20 – 0.06	0.261	44.00	-0.05	0.02	-0.08 – -0.01	**0.010**	51.00	-0.11	0.06	-0.23 – 0.00	0.055	51.00
Random Effects																				
σ^2	0.00					0.03					0.00					0.03				
τ_{00}	0.00_{Island}					0.00_{Island}					0.00_{Island}					0.00_{Island}				
ICC	0.25																			
N	3_{Island}					3_{Island}					3_{Island}					3_{Island}				
Observations	50					50					57					57				
Marginal R^2 / Conditional R^2	0.187 / 0.387					0.175 / NA					0.197 / NA					0.151 / NA				
AIC	-112.188					-29.720					-168.361					-33.912				

<u>Table 1.</u> Showing descriptive statistics of linear mixed effects models of change through DHW event greater than 10.

<u>Cumulative DHW Stress</u>

A regional mixed effects model, with island as random factor and reef type as both random and interactive term with cumulative DHW stress, showed that cumulative DHW is a significant predictor of the change of *Acropora* (LME, P<.01, Table 2) (χ^2:9.7, P<0.05, Δ AIC: 3.7 comparing mixed model with the null mixed model) but not *Porites* (LME, P>.05, Table 2) (χ^2:16.1, P<0.01, Δ AIC:10.1). Increased DHW stress negatively affected both, but contextually based upon reef type (Figure 12, Table 2). *Acropora* on outer windward reefs was most impacted by increasing DHW stress (estimate of random effect on slope =-0.3), with notably variability among the islands whereby Yap windward reefs exposed to medium DHW stress showed less mortality than expected (Figure 12). *Acropora* decline on other reef types was similar and more gradual with lower effect sizes (estimates of random effects = -0.07, -0.06, -0.02) *Porites* on outer leeward, outer windward, and patch/back reefs may increase under low levels of DHW stress, however, will decrease with medium to high levels of DHW stress (Figure 12). *Porites* on outer leeward reefs were most susceptible to increases in DHW stress (random effects=-0.2). *Porites* on inner reefs may slightly increase with the medium to high DHW stress that was observed in this study (random effects= 0.2).

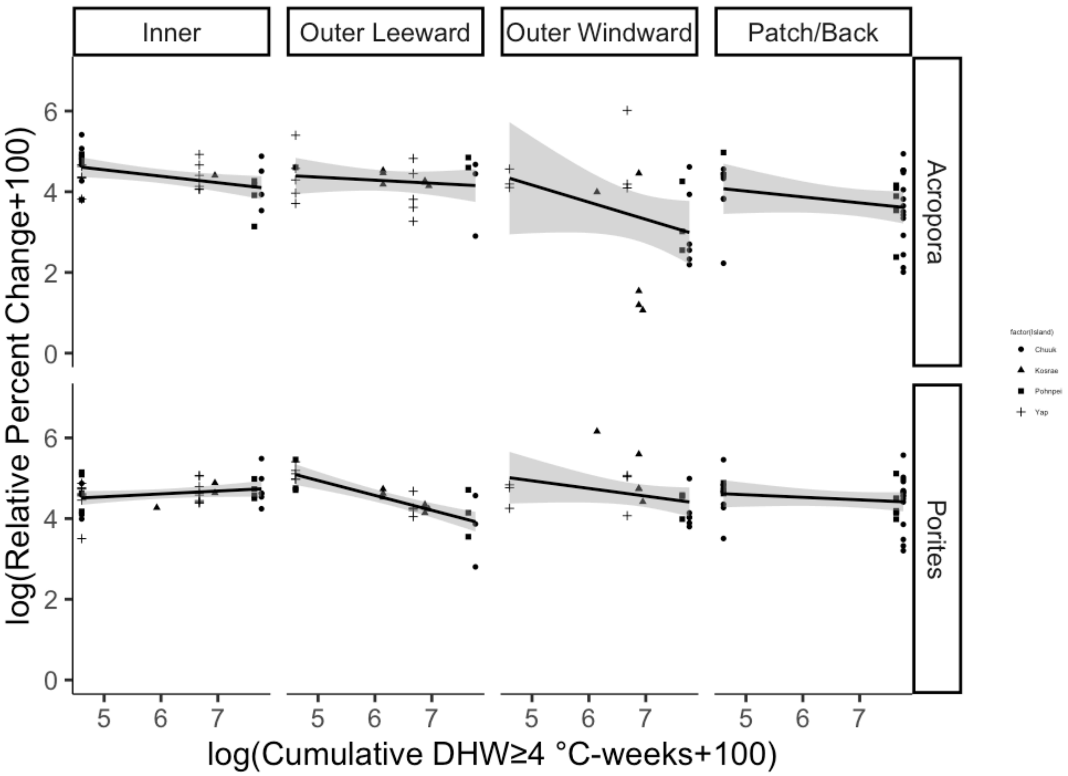


Figure 12. The relationship between relative percent change and cumulative daily DHW greater than or equal to four (4). Note graphic depicts, the x and y axis with transformed values and a constant of 100 added, thus, any value less than 4.6 were negative change values (ie losses) in total coral cover while any values greater than 4.6 were a positive change values (ie increases) in total coral cover.

	Acropora.Relative.Change					**Porites.Relative.Change**				
Predictors	*Estimates*	*std. Error*	*CI*	*p*	*df*	*Estimates*	*std. Error*	*CI*	*p*	*df*
(Intercept)	5.31	0.42	4.47 – 6.14	**<0.001**	92.00	5.29	0.48	4.35 – 6.24	**<0.001**	111.00
DHW sum	-0.21	0.07	-0.35 – -0.06	**0.006**	92.00	-0.12	0.08	-0.27 – 0.04	0.143	111.00
Random Effects										
σ^2	0.64					0.21				
τ_{00}	0.04 $_{Reef.Type.2}$					0.72 $_{Reef.Type.2}$				
	0.00 $_{Island}$					0.00 $_{Island}$				
τ_{11}	0.01 $_{Reef.Type.2.DHW.sum}$					0.02 $_{Reef.Type.2.DHW.sum}$				
ρ_{01}	-1.00 $_{Reef.Type.2}$					-1.00 $_{Reef.Type.2}$				
N	4 $_{Reef.Type.2}$					4 $_{Reef.Type.2}$				
	4 $_{Island}$					4 $_{Island}$				
Observations	99					118				
Marginal R^2 / Conditional R^2	0.106 / NA					0.106 / NA				
AIC	256.523					172.555				
AICc	257.754					173.574				

Table 2. Showing descriptive statistics of linear mixed effects models of cumulative DHW greater than 4 and relative change of genus cover.

Discussion

Micronesian coral reefs have been exposed to growing local and global stressors which have led to substantial changes over the past decades (Houk *et al.* 2015, Houk *et al.* 2020a, McLean *et al.* 2016, van Woesik & Cacciaplagna 2019). However, inconsistent data collection and limited formal documentation have led to shifting baselines that may have masked our ability to appreciate spatial and temporal changes. This study used unique historic and recent assessments to better understand ecological change by focusing on the two most prolific genera, *Acropora* and *Porites*, which have contrasting life histories. By incorporating historic data this study shows that Micronesian outer reefs were dominated by *Acropora* corals during the 1980s, predominantly staghorn/arborescent and plating growth forms. This is in accordance with other historic studies in the region that predate large disturbances (Randall 1973, Turak & DeVantier 2005, McLean *et al.* 2016). It is also consistent with studies from the Caribbean, where historical dominance by *Acropora* for millennia was recently lost, following disease and bleaching (Greenstein et al. 1998, Aronson & Precht 2010). Meanwhile, the earliest timepoints available for this study revealed inner and patch/back reefs were already dominated by *Porites* communities, however, showed more heterogeneity with key representation of *Acropora* growthforms*,* particularly the staghorn/arborescents. The broadscale outer versus inner reef dominance of *Acropora* versus *Porites*, respectively, was to be expected as environmental factors have been shown to be historic drivers of coral reef communities (Done 1982). For example, outer reefs are slightly more oligotrophic and receive more wave energy than inner reefs (Done & Potts 1992) In contrast, sheltered more nutrient rich waters on inner and patch/back reefs may favor slow growing more heterotrophic *Porites* (Potts *et al.* 1985).

Comparisons between the earliest data and the late 2000's revealed that Micronesian reefs had already begun drastically changing, most likely due to increased local disturbances and chronic stressors including COTS, land-based pollution, and fishing pressure (Houk *et al.* 2015, Houk *et al.* 2012, Golbuu *et al.* 2008) and by the mid 2010s, these stressors led to the ecological separation outer reef coral communities into two predictable geographical zones across the region: windward reefs dominated by *Acropora* growthforms and leeward reefs dominate by *Porites* growthforms. This shift from a historically more even spatial distribution, to distinct separate community structure had been previously observed for the island of Kosrae (Mclean et al. 2016) and is now being recognized as a consistent general pattern across the region. Meanwhile, the growing dominance of *Porites* and its growth forms on inner reefs continued into the mid 2010s, while nearly all representation of *Acropora* growth forms were lost, suggesting these inner reefs were most susceptible to the combination of these local stressors. *Acropora* on patch/back reefs was gradually declining, however, maintained slightly higher cover and more heterogenous *Acropora/Porites* assemblage structure.

In the late 2010s reefs faced a new threat from unprecedented exposure to novel DHW stress. During this time period the last remaining large populations of *Acropora* were heavily impacted and all reef types declined to less than 1% total *Acropora* cover. In particular, the staghorn/arborescents and plating growth forms that were once principal contributors to Micronesian outer reefs were most impacted and they became only minor contributors to coral assemblages in the most recent time period. While *Porites* was impacted by DHW stress as well, moderate cover of *Porites* was able to persist through these stress events. Within *Porites* there has been a striking rise in dominance of a particular species complex, *Porites rus*. *Porites rus* has become the first or second major contributor across all reef types. Shifts to this tolerant species, *Porites rus*, have been seen in nearby islands in the Central pacific (Donner and Carilli 2019). Other coral community shifts to single species *Porites* assemblages, are not unique to the central/west Pacific and have also been seen in the Caribbean, where dominance of *Porites astreoides* following multiple stressors was also observed (Green *et al.* 2008).

The composition of focal genera on reefs prior to a strong DHW event was shown to be a key predictor of change in total coral cover through a strong DHW event. Reefs dominated by *Acropora* appeared more susceptible and reefs dominated by *Porites* more resistant to change in total coral cover through a strong DHW stress event (>10). Thus, integration of taxonomic indicators is necessary to provide a more holistic understanding of these ecosystems and their functionality (DeVantier *et al.* 1998, Alvarez-Filip *et al.* 2013) and studies examining only coral cover trends and that fail to incorporate any taxonomic indicators may likely mask ecological change (Bruno and Selig 2007).

Further, the magnitude of degree heating weeks stress proved to be a significant predictor of the decline of *Acropora* in a region model, with the most vulnerable reef type being outer windward reefs. While *Porites* was much more tolerant of DHW stress, this tolerance was dictated by spatial distribution and the degree of DHW stress. For example, *Porites* was particularly tolerant to DHW stress on inner reefs which slightly increased through the 2016-2017 events. However, on outer leeward reefs, low levels of DHW stress may favor *Porites* growth and dominance, while DHW above 10 will cause even these stress tolerant genera to decline. Following DHW stress events of 2016-2017 across the region, Micronesian reefs are currently in a *Porites* dominated state which will likely have many implications for the Micronesian region.

Future of Micronesian reefs

The clear and consistent spatial patterns of the coral communities transitioning from *Acropora* to *Porites* will have significant implications for the future of Micronesian reefs. In the short term, it appears that some Micronesian reefs may be able support moderate coral cover in some areas, potentially providing some remnants of past ecosystem services. However, this transition to *Porites* and its less complex growth forms will cause an overall decrease in reef calcification and reef rugosity (Courtney *et al.* 2020, van Woesik & Cacciaplagna 2019). Lower calcifications rates and reef complexity offer less in terms of buffering wave energy and protecting shorelines (Alvarez-Filip et al. 2009). The loss of structurally complex and fast growing *Acropora* and replacement with non-branching *Porites* due to DHW stress is of particular concern on windward sides of islands which are essential for protecting communities from wave and storm damage. While it is predicted that *Porites* will be the most resistant coral and least impacted by DHW stress, its life history traits make it vulnerable to other climate change impacts. For example, it is predicted that sea-level rise will continue and while fast growing *Acropora* communities may be able to keep up with this rise, slow growing *Porites* corals will most likely not be able to (van Woesik et al. 2015). Additionally, following intense storms or other acute disturbances it could take much longer for slow growing *Porites* communities to recover, leaving historically Scleractinia dominated reefs vulnerable to phase shifts to faster growing non-scleractinian benthic organisms (Norstrom et al. 2009).

The loss of the speciose and structurally complex *Acropora* will most likely have ramifications on fish and reef associated biodiversity as well (Booth & Beretta 2002). For example, following the loss of *Acropora* to a bleaching event on the Australian GBR, a decrease in the abundance and diversity of reef associated damselfish and corallivorous butterflyfish has been observed (Booth & Beretta 2002, Pratchett et al. 2008). While this loss may seem trivial, the loss of these smaller reef associated fish could have trophic implications for larger more commercially and subsistence valued fish, in turn affecting food security, human health and nations' Gross Domestic Product (GDP) (Pratchett 2008).

Resistance and recovery

Predicting if or where *Acropora* will persist is challenging, as it may be dictated by a variety of factors including the return time of stress events, herbivorous fish biomass, favorable recruitment substrates, number of juveniles, and number of reproductively viable colonies (Gouezo *et al.* 2019). Prior to the DHW stress events, the relatively high cover of *Acropora* on windward reefs may have been acting as a source population, facilitating recovery at the island scale by providing larvae across reef types. However, these populations were devastated in the 2016-2017 DHW events and in 2019-2020 all reef types were supporting less than 1% *Acropora* cover. Thus, this lack of a large reproductively viable source population may slow recovery time by limiting production and dispersal of larvae (Golbuu et al. 2012). Prior to DHW stress events, local factors seemed to slightly favor persistence of *Acropora* on outer windward and patch/back reefs, as some remnants of *Acropora* continued to remain on these reef types following the DHW stress. Although minor, given *Acropora's* fast growth rate, cover may be able to recover in these habitats first. However, due to these reef types particular susceptibility to DHW stress, the recovery dynamic of this genus may ultimately be dictated by the frequency and intensity of DHW events and other disturbances in the future, and the ability for thermal adaptation and other forms of adaptation (Guest et al 2012). *Acropora* are unlikely to persist or recover on inner and outer leeward reefs due to the continued impacts from local stressors combined with potential future DHW stress events.

Local factors seemed to be driving the regional dominance *Porites* across reef types up until the DHW of 2016-2017. While *Porites* populations persisted following these DHW events, this study shows that even this stress tolerant genus may be threatened if the frequency and intensity of DHW stress events continue. Additionally, as human population rises, other local stressors may continue to increase in intensity. This is of concern because increasing levels local stressors, such as fishing pressure and nutrient pollution, have been seen to act synergistically with heat stress to detrimentally affect corals (Donovan *et al.* 2020, Donovan *et al.* 2021). Last, it was shown that there is a striking recent rise in dominance of a particular by a singular species complex, *Porites rus*. This low coral diversity on future Micronesian reefs may have many implications, including leaving reefs vulnerable to biotic stressors, such as disease outbreaks, which have yet to be a major issue in the region (Aronson & Precht 1997). In sum, management of local and global stressor in necessary to maintain coral dominated ecosystems in Micronesia.

Conclusion

In many regions it is generally accepted that there has been a shift from sensitive to more stress tolerant coral species. Still, this thesis aimed for a more in depth understanding of the two most prominent coral genera across spatial and temporal scales which are often overlooked. In the absence of DHW stress, Micronesia may be able to support moderate coral cover reefs dominated by *Porites*, maintaining some remnants of past reef functionality. However, when local stressors are combined with DHW stress, *Acropora* may lose their largest remaining populations on the outer east coast and even the most stress tolerant genus, *Porites*, may not be able to persist in its current favored locations. Coral reef resource managers should use the information presented in this thesis to guide the development of coral reef management strategies such as marine protected area design and coral restoration which require ecological context of past and present coral community compositions for effective implementation. Future studies should combine acute stressors presented in this study with additional metrics of chronic local stressors, to determine management thresholds which can be used to best support persistence of coral communities under current scenarios of climate change and associated disturbance frequencies.

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