EXAMINING PREDICTED VERSUS OBSERVED CORAL REEF RESILIENCE IN CHUUK, MICRONESIA

BY

CHRISTINA M. STARSINIC

A thesis submitted in partial fulfillment of the
requirements for the degree of

MASTER OF SCIENCE

IN

BIOLOGY

SUPERVISORY COMMITTEE
Dr. Peter Houk, Chair
Dr. Laurie Raymundo, Member
Dr. Robert van Woesik, Member

UNIVERSITY OF GUAM

DECEMBER 2021

Abstract

Rapid assessments of coral-reef resilience have been conducted throughout Micronesia during the past decade to predict which reefs might be most vulnerable to climate-induced disturbances that are becoming more frequent. Warm-water mass bleaching events have occurred throughout parts of Micronesia in 2013, 2014, 2016, and 2017, so it is now desirable to examine the relationship between observed trends from long-term monitoring programs documenting reef condition through time and rapid assessments of resilience conducted prior to disturbances. This study examined these relationships in Chuuk, Federated States of Micronesia, where a rapid-assessment study was conducted in 2016 just before a major heat stress event, and long-term monitoring has been ongoing since 2012. Uniquely, this thesis had the opportunity to examine reefs where both long-term data and rapid resilience studies were conducted. Three metrics were selected from long-term data to depict the status of reefs through time: 1) coral richness, 2) non-*Porites* coral cover, and 3) a non-coral benthic-substrate ratio describing calcification potential. These were selected because they represent different and influential processes related to reef functioning. The 2016 heat stress event impacted reef status metrics but to different degrees and with different spatial patterns. The rapid-assessment study was found to identify unique assemblages where high coral cover and diversity existed; however, these reefs were also most susceptible to ecological change following bleaching. Thus, the rapid study predicted the opposite to what has been observed from the long-term studies when examining island-scale trends. *Porites* dominant reefs that are tolerant to stress showed little change across the thermal-stress event but were originally predicted to have low resilience. In contrast, diverse reefs, predicted to have high resilience, were altered by the thermal-stress event. When stratified by reef type to control for some of the inherent variation, poor relationships between predicted versus observed resilience remained for differing reasons. It is plausible that the poor relationships stemmed mainly from the rapid-assessment study using equal weighting of variables describing daily environmental conditions and reef states, as many studies serve to highlight non-equal, hierarchical influences of local stressors on reef resilience. However, partial correlations revealed that disease presence and physical reef characteristics from the rapid assessment werethe most accurate metrics associated with resilience. Prioritizing biological indicators for use in rapid resilience assessments, instead of environmental factors which serve as drivers of the reef systems, appeared to be the best approach to benefit resilience assessments into the future. Additional studies could then determine how environmental regimes might predict ‘resilience’ to best inform management of potential scenarios that may unfold. This will allow scientists to identify conservation efforts that are expected to benefit the reef system in Chuuk, Micronesia, and beyond.

Keywords: *coral reef, resilience, richness, benthic substrate ratio, Micronesia*

Acknowledgements

First, to my mom, Marie, for your unending love and support during this journey. You and Dad's encouragement throughout my life has given me the confidence to chase my dreams and the determination to conquer the challenges I've encountered along the way. To my brother, Travis, thank you for always being someone I could look up to and never hesitating to tell me to "go for it." To my friends around the world, I could not have done this without the late-night phone calls, coffee runs, and endless pep talks.

My sincerest thanks to my ever-dedicated advisor, Dr. Peter Houk, for your patience, inspiration, and guidance through these past few years. I would truly not be the scientist I am without you. To my committee members Dr. Laurie Raymundo and Dr. Rob van Woesik, thank you for your unwavering support and flexibility that has allowed me to reach beyond my own expectations and to be successful even during an unconventional thesis process. Also, I would like to acknowledge all the students, faculty, and staff of the UOG Marine Lab. The knowledge I've gained and the memories I've made are immeasurable. Additionally, thank you to the many people who I worked with on my trips throughout Micronesia, without whom this project never would have been possible. A special thanks to The Nature Conservancy, Micronesia Challenge, Micronesia Conservation Trust, NOAA Coral Reef Conservation Program, and the Chuuk Conservation Society.

Finally, thank you to the Research Corporation of the University of Guam for funding this project and my time at the UOG Marine Lab.

Table of Contents

List of Tables

List of Figures

Introduction

Coral reefs are complex systems providing environmental, cultural, and economic benefits to society through fisheries, tradition, cultural practices, coastal protection, and tourism (Moberg and Folke 1999, Bellwood et al. 2004). Over the past 20 years, these ecosystems have fallen under increasing threat of anthropogenic stressors and climate change (Hoegh-Guldberg et al. 2007, Cinner et al 2013). Human-caused impacts such as declining water quality from pollution and sedimentation, overfishing, and physical destruction from boats, blast fishing, and harvesting have altered the composition and structure of coral reefs worldwide, making these ecosystems more vulnerable to natural disturbances (Bellwood et al. 2004). Disturbances such as climate-induced bleaching from elevated sea-surface temperatures and outbreaks of predators, such as *Acanthaster planci,* represent acute events that dramatically decrease the amount of living coral on reefs (Obura and Grimsditch 2009). Local stressors such as fishing pressure and pollution represent chronic stressors that reduce the capacity for reefs to recover from acute disturbances (Obura and Grimsditch 2009). While acute disturbances cause dramatic effects over short time periods, chronic disturbances effect resistance and recovery, together known as resilience (Bozec and Mumby 2015, Nystrom et al. 2000). In sum, chronic stress decreases the resilience of coral reefs and makes them more susceptible to acute disturbances (Bozec and Mumby 2015, Nystrom et al. 2000)

Resilience can be described as the ability to withstand stress, resist phase shifts, and recover from disturbance events (West and Salm 2003, Holling 1973, Bellwood et al 2004, Nystrom and Folke 2000). An increasing number of studies have begun investigating the resilience potential of coral reef ecosystems and have hypothesized biological indicators that are expected to correlate with resistance and recovery (Green and Bellwood 2009, Obura and Grimsditch 2009, Bellwood et al 2004, Rowlands et al. 2012). In turn, key biological factors that increase the capability of a reef to withstand and rebound from disturbances have been combined to define ecological resilience (Nystrom 2006, West and Salm 2003). Research continues to focus on identifying both biological indicators and environmental drivers that are thought to enhance either resistance or recovery (Graham et al. 2015, McClanahan 2012). There is, however, a lack of clarity on which indicators, or sets of drivers, are most relevant to resilience. Over 60 different indicators have been proposed across different studies, including fishing pressure, herbivore biomass, coral cover, and temperature variability (McClanahan 2012). Some indicators are thought to influence resistance while others are thought to influence recovery.

Resilience studies have been developing since the early 2000s, but approaches are highly varied (Nystrom et al. 2008). Some studies utilize SCUBA to extensively monitor coral, fish, and algae populations (Maynard et al. 2012). Others analyze satellite imagery to focus on the roles of reef complexity, water temperature, and chlorophyll-a concentrations (Knudby et al. 2013). Despite the diversity of approaches used to generate resilience metrics, only rapid assessment studies have been used thus far (Cinner et al. 2013, Heenan and Williams 2013, Maynard et al. 2015). Rapid assessment studies use data over a short timeframe to evaluate the state of a reef and attempt to predict the future state of the reef (Mumby et al. 2012). It is less clear whether rapid assessment studies are useful in successfully predicting future trends in reef assemblages and which metrics of reef resilience studies are most useful for predicting resilience.

Table 1: Resilience indicators utilized by rapid assessments of resilience.

Resilience Indicator	Justification	Citation
Coral Diversity	Functional redundancy	McClanahan et al. 2012
Coral Recruitment	Replenish populations	McClanahan et al. 2012
Coral Disease	Causes coral mortality, lowers resistance to other stressors	McClanahan et al. 2012, Bozec & Mumby 2015
Herbivore Diversity	Functional redundancy, herbivores feed on various algae size/type	McCleod 2019, Elmquist et al. 2003
Herbivore Biomass	Control algae growth	Elmquist et al. 2003
Benthic Ratios	suitable substrate for coral settlement, good colonizers vs. bad - good for habitat and reef framework; bad prevents settlement.	McClanahan 2012, Nystrom et al 2008
Macroalgae cover	Inhibit coral larval settlement, trap sediment, correlate with negative density of recruits	Elmquist et al. 2003, McClanahan 2012, Mumby 2012
Temperature Variability	Temperatures fluctuate differently in varying locations. Areas exposed to greater fluctuations may contain more resistant corals.	McClanahan et al. 2012
Chlorophyll Levels	shows ecological fluctuations, phytoplankton biomass - indicates nutrient levels, can cause outbreaks of coral predators	Otero & Carbery 2004, Riegl et al. 2014
Wave Action/Exposure	causes vertical mixing,	Obura & Grimsditch 2009, Graham et al. 2015
Habitat Complexity	contributes to diversity and productivity, structure for coral growth	Graham et al. 2015, Maynard et al. 2015
Fishing Accessibility	Overfishing, reduce large predators to small herbivores, less algal control	Elmquist 2003, McClanahan et al. 2012
Management/Jurisdiction	Protected areas, no take zones	Mumby et al. 2012
Size - class distribution	redundancy	Nystrom et al 2008
Connectivity	spread of traits to replenish areas, and maintain ecosystem; spatial variation and recruitment	Nystrom et al 2008, Maynard 2015, McClanahan et al. 2012

In 2016, a unique project facilitated the development of a rapid assessment in Chuuk, Federated States of Micronesia at the same sites where long-term monitoring efforts have existed since 2012 (Salm et al 2016). The year after the rapid assessment, a significant coral bleaching event was evident across Chuuk reefs (NOAA 2017), providing the basis for the present comparison of expected versus observed resilience. Chuuk reefs are also part of a regional, long-term monitoring effort across Micronesia. Sites examined during the rapid assessment had a history of standardized monitoring data and were surveyed for both rapid assessment and long-term monitoring during the 2016 project. For these reasons, Chuuk is perfect to examine the relationships between the rapid assessment study and longer-term trends derived from a standardized coral reef monitoring program (Houk et al. 2015). The general question being addressed is: What is the relationship between predicted resilience from rapid assessment studies and longer-term trends across disturbances? In order to fully answer this question, a suite of more specific questions was explored, including: (1) Are there inherent differences between habitats that may affect their resilience metrics? (2) What individual biological metrics can be used to describe the trends in reef 'condition' (Houk et al. 2015, McClanahan et al. 2012, Mumby 2014)? (3) Does initial 'condition' affect post-disturbance trends? (4) Does the relationship between resilience and observed reef trends vary across habitats?

Methods

Study Site

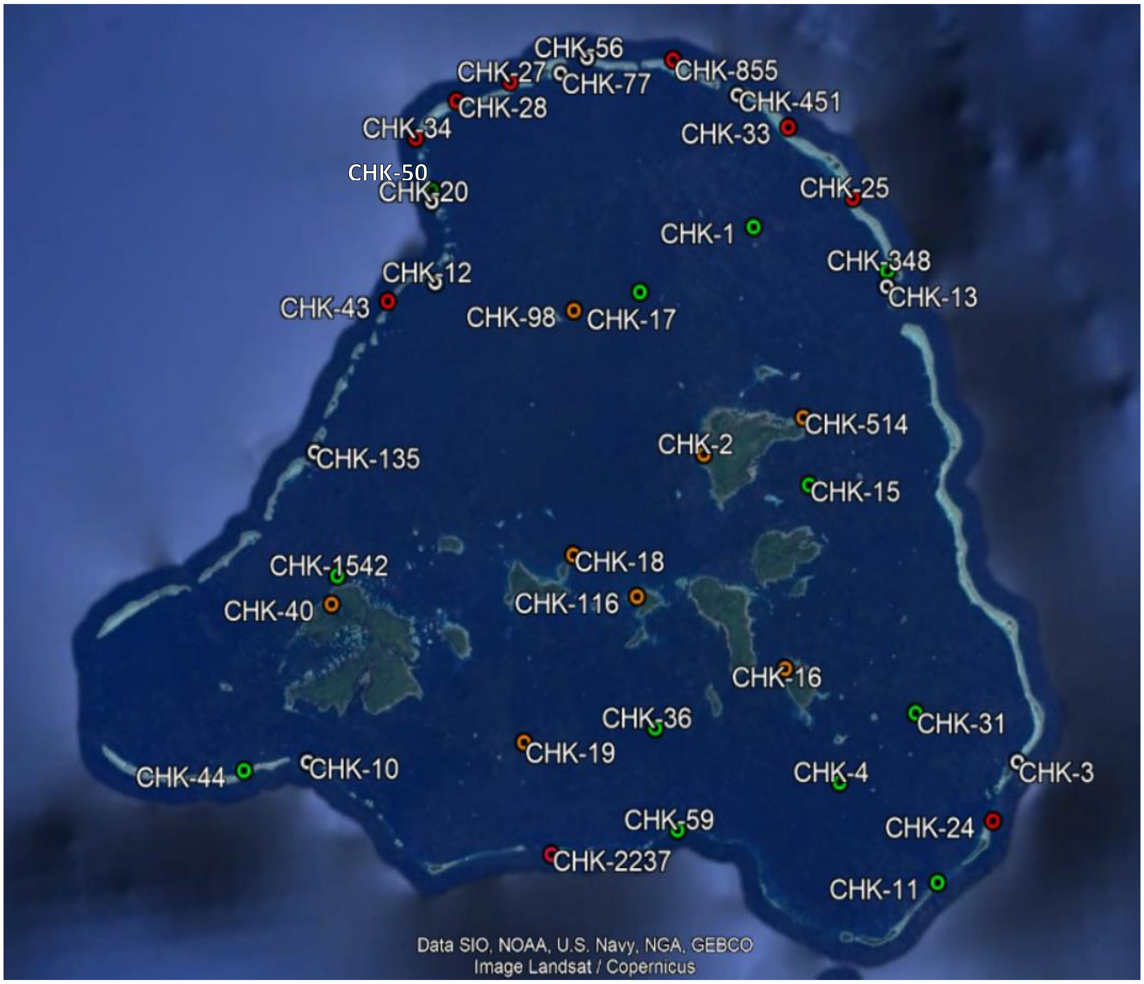
This study examined predicted resilience verses observed reef trends across Chuuk lagoon, Federated States of Micronesia. Study sites were distributed across all major reef types and wave exposure regimes as part of the long-term monitoring program design (Houk et al.

2015). A total of 38 reefs have been monitored both before and after the bleaching event associated with the 2015–2016 El Nino (Houk et al. 2020). These sites were evenly distributed across four reef types: outer, inner, channel, and patch/back reefs (Figure 1). These reefs were also surveyed in a recent rapid-assessment resilience study that was conducted in 2016, prior to bleaching, thereby allowing for a direct comparison of predicted resilience versus observed trends (Figure 2).

Chuuk has a growing network of no-take MPAs, and some now have formal management that includes widespread education and law enforcement. However, there is limited enforcement and species-based policies are just now starting to evolve (Cuetos-Bueno 2012, Houk 2015). Therefore, a gradient of high-to-low fishing pressure exists across our study sites that represents the dominant chronic stressor for Chuuk reefs, with uncertain potential influences on resilience (Cuetos-Bueno et al. 2018).

Rapid-assessment study of resilience

In 2016, a resilience study by Rodney V. Salm et al., with The Nature Conservancy, collected data from 79 sites across Chuuk lagoon. Data were collected during 20 minute *in situ* surveys at both 8-12m and 3-5 m depths. A series of subjective resilience indicators were recorded by trained divers (see Figure 3 below). Each indicator was evaluated using an ordinal scale and categorized as being attributed primarily to resistance or recovery. Two extra categories, disease and predation, were also included (see Figure 3 below). The scores for each indicator were added together and then averaged across depth to create a site-based resilience score. All indicators were scaled in a low-to-high manner to represent bad-to-good for predicted



Data SIO, NOAA, U.S. Navy, NGA, GEBCO
Image Landsat / Copernicus

Figure 1: Study sites in Chuuk, Micronesia.

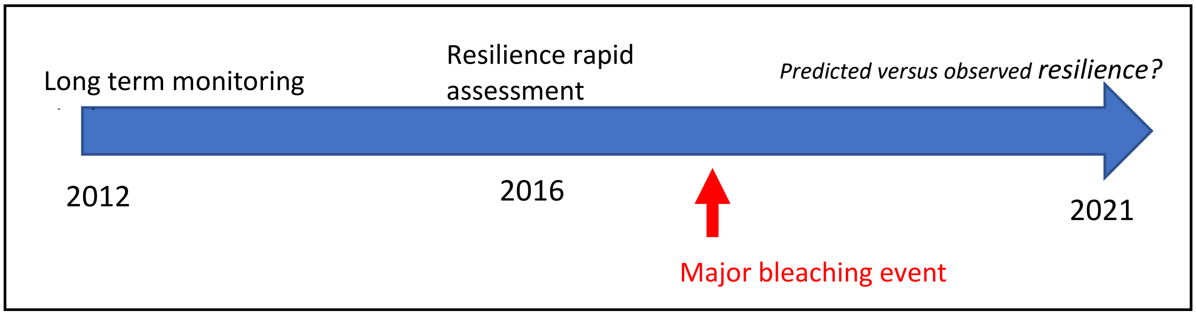
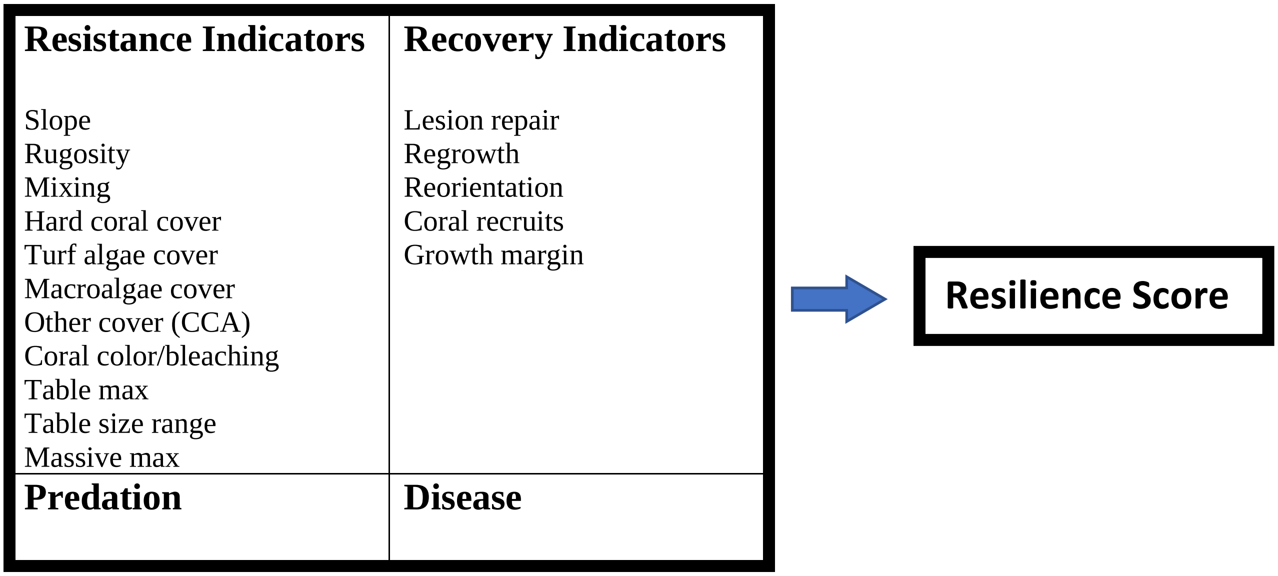


Figure 2: Timeline of Chuuk monitoring, resilience studies, and bleaching event.



Resistance Indicators	**Recovery Indicators**
Slope Rugosity Mixing Hard coral cover Turf algae cover Macroalgae cover Other cover (CCA) Coral color/bleaching Table max Table size range Massive max	Lesion repair Regrowth Reorientation Coral recruits Growth margin
Predation	**Disease**

Figure 3: Scoring resilience in 2016 rapid assessment study by Rodney V. Salm et al. (2016). Indicators placed in two main categories (i.e. resistance and recovery) with additional, individual, categories of predation and disease. Resilience Score used to represent "predicted resilience" for current study.

resilience. For example, high disease presence was given a value of 1 whereas low disease presence received a 3. These scores are referred to as “predicted resilience” in the present study.

Long-term monitoring

A standardized, long-term coral reef monitoring program has been collecting data across Chuuk since 2012 (Houk et al. 2015). Study sites are visited every 2-4 years with most sites having been visited in 2016 and 2019. Five 50-m line transects were used for evaluating coral and benthic substrates at a depth of 8−10 m for outer-reefs and 3−5 m for inner reefs. Benthic substrates were evaluated using photo-quadrats. Fifty photos were taken at 1-m intervals along each 50 m transect. CPCe (Coral Point Count with Excel extension) programming was utilized to evaluate percentages of macro and turf algal cover, coral-genus richness, and cover of crustose coralline algae (Kohler and Gill 2006).

Data on coral assemblages were collected from 10 replicate 1 m^2 quadrats that were tossed at equal intervals along the transect lines. All coral colonies whose center point resided in the quadrat were measured by determining the maximum diameter and the diameter perpendicular to the maximum. The corals were identified to the highest taxonomic resolution possible, typically genus plus growth form or species. All coral data were collected by two trained observers across the years.

Preliminary analyses of reef types

Rapid assessments typically investigate resilience at an island-wide scale, with little to no mention of reef types (Mumby et al. 2012). However, reef type habitats have inherent differences based upon biological, environmental, and anthropogenic factors, such as variation in wave exposure, pollution levels, and biological assemblages which could affect resilience potential (Houk et al. 2012, Salm et al. 2016). In order to test for inherent variation between reef types in Chuuk, a multivariate analysis and ordination were conducted on site-based, pre-disturbance, benthic data averaged across 2012−2016. This process examined the potential for reef types to support distinct assemblages. Data were aggregated to the site level and a Bray-Curtis similarity matrix was created to calculate site-based distance matrices. These matrices were plotted using a Principal Component Ordination (PCO), and formal tests of significance were conducted using a PERMANOVA and subsequent pairwise testing (Clarke and Gorley 2015).

Biological metrics to define reef ‘condition’

Prior to evaluating the ability of rapid-assessment studies to detect trends in reef assemblages, this study identified metrics to define reef ‘condition’ through time that were less sensitive to disturbances and resonated with the functional processes of calcification and early recovery of the coral assemblage. The univariate metrics chosen have a long history of investigation and have been used in reef monitoring efforts across the globe (Houk 2015, McClanahan et al. 2012, Mumby et al. 2012, Nystrom 2008).

The first metric was a benthic substrate ratio that compared percentage cover of calcified substrate with non-calcified substrate (i.e. macroalgae and turf algae). Benthic substrate ratios provide a repeatable means to capture carbonate production potential, which is a fundamental process on reefs, while not being influenced by coral cover that varies due to uncertain disturbance histories (Lange et al. 2020, Perry et al. 2012). Beyond carbonate production, coral recruits prefer a clean hard surface, clear of sediment and turf to settle and grow (McClanahan et al. 2012). Crustose Coralline Algae (CCA) contribute to the calcification process and often provides the ideal substrate, whereas turf and macroalgae may prevent both settlement and growth (Webster et al. 2013, Heyward and Negri 1999). Without preferential substrate for coral settlement, the function of the reef may be compromised, resulting in a phase shift and, eventually, loss of carbonate production (McClanahan et al. 2012). A resilient reef retains a state suitable for corals to thrive and is expected to have a higher proportion of CCA and clean substrate compared with a non-resilient reef. For these combined reasons, a benthic substrate ratio that concisely describes the non-coral, benthic state of each reef was used as the first indicator of ‘condition’ through time.

While many studies have documented decreases in coral cover, some recent studies have investigated the significance of taxonomic shifts in corals and the significance of lowering species richness on reefs (Alvarez-filip et al. 2013, Berumen and Pratchett 2006, Aronson and Precht 1997). Species transitions are complex and somewhat site-specific (Schmitt et al. 2019), however predictable responses appear to exist within each site. Studies have found that when a disturbance event occurs and coral cover is lost, the initial response should be a relatively higher diversity of new recruits on healthy, recovering reefs (Hughes and Connell 1999). In summary, the loss of coral is expected to open space on the reef and pave the way for more diverse assemblages of recruits. Therefore, this study utilized the parsimonious diversity measure of species richness as the second metric of reef ‘condition’. Specifically, genus plus growth form (genus-growth) was utilized to classify corals to the lowest, most confident, taxonomic level. Richness is ideal because it builds upon the benthic substrate ratio that defined that state of benthic substrates, which are characteristics accepted to improve resilience (Houk et al. 2016, Nystrom et al. 2008).

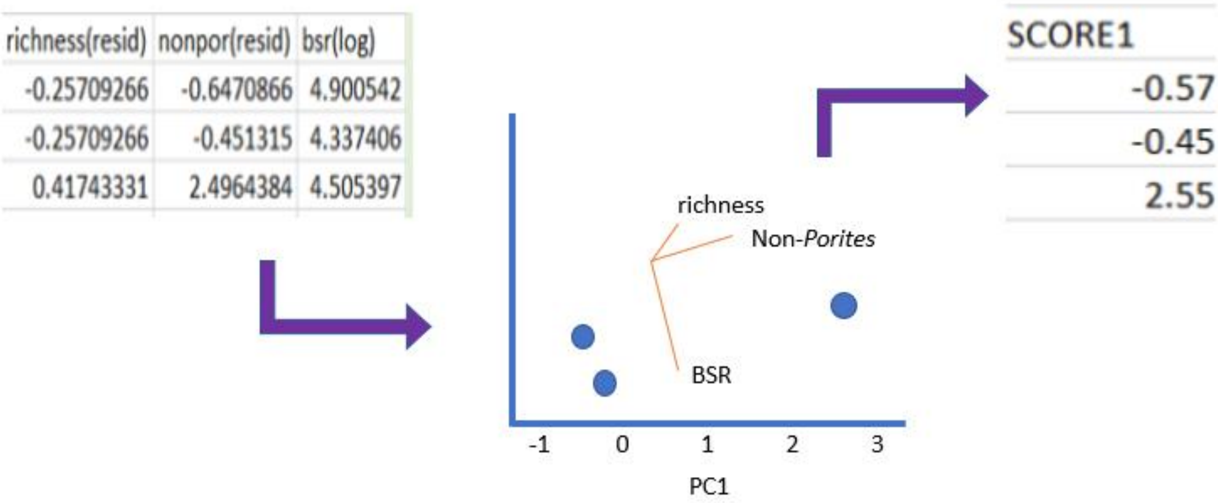
Third, the proportional contribution of non-*Porites* corals to total coral cover was evaluated. Poritids are a slow growing genus that have shown to be less susceptible to high temperature disturbances (Marshall and Baird 2000). In multiple studies investigating susceptibility across coral genera, *Porites* routinely rank as the most resistant to bleaching (Pratchett et al. 2013, Marshall and Baird 2000, Burt et al. 2011). Other genera, such as fast growing, branching *Acropora,* provide essential framework and structure to reefs. However, these species are also highly sensitive to thermal stress (Hughes et al 2010). Therefore, studies have often documented a shift in coral assemblages towards high proportions of *Porites* (Pratchett et al. 2011). Thus, the relative change in proportional contribution of non-*Porites* corals through disturbance-and-recovery events is also expected to be a good indicator of reef ‘condition’ through time and builds upon both healthy substrates and species diversity (Pratchett et al. 2011, van Woesik 2011, Hughes et al. 2010).

In order to define reef ‘condition’ at each site, the biological metrics were assessed by evaluating the overall percent change in each metric: benthic substrate ratio, generic richness, and non-*Porites* contribution, for 38 sites from pre-disturbance to post-disturbance time frames. Percent change was used to account for site-by-site variation in assemblages and to compare proportional changes. Because percent change has the potential to be influenced by extreme low values, multiple tests to identify outliers were conducted. However, no statistical outliers were determined. Overall percent change was utilized in order to investigate the full shift of the reef from a pre-disturbance to post-disturbance state with a short recovery period. These values were checked for normality and then log transformed when necessary.

Reef trends

The goal of this study was to calculate a single metric summarizing long-term trends in the reef state, then compare the metric of long-term trends against predicted resilience. Long-term trends for each metric, described above, represented the percent change from the earliest to the most recent data. A principal component analysis (PCA) was then performed to create a single variable from the percent change of all three metrics (Figure 4). From this, the primary principal component axis score (PC1) was derived and assigned as the univariate metric describing reef change through time (Figure 3). These values were normalized to match the normalized predicted resilience scores from the rapid assessment. Reef-trend values were normalized on the island scale to allow for a direct comparison to predicted resilience score from the 2016 study and for each reef type separately to provide multiple comparisons and account for habitat variation.

In some instances, the percent change in the three reef metrics was adjusted prior to calculating PCA scores. These adjustments were made to remove any potential bias of differing starting points in ecosystems states. Studies on a variety of ecosystems have revealed that starting states can predict the change following a disturbance. In particular, systems that have a higher starting point stand to lose more (Allison 2004, Pfisterer and Schmid 2002). These studies only speculate on the processes behind these results, but lower genetic diversity in climax communities may lead to a more unified response following disturbance (Pfisterer and Schmid 2002). Additionally, systems with greater diversity often include more sensitive species that suffer greater loss (Allison 2004).



richness(resid)	nonpor(resid)	bsr(log)
-0.25709266	-0.6470866	4.900542
-0.25709266	-0.451315	4.337406
0.41743331	2.4964384	4.505397

SCORE1
-0.57
-0.45
2.55

Figure 4: Example of forming resilience score from PCA of 3 metrics of residuals and log transformed values.

In order to determine when starting states for the three chosen metrics were influential, this study performed a regression analysis between the starting value of each metric (independent variable) and the percent change (dependent variable). If significant regressions existed, the residuals of the dependent variable were calculated and used instead of raw percent changes.

Comparing resilience scores

Finally, observed resilience scores derived from long-term trends were compared with the predicted resilience scores calculated by the 2016 rapid-assessment study. At the island scale, a kriging process was used to visualize the distribution of observed-versus-predicted resilience scores. Kriging utilized the measured values of resilience to predict unmeasured regions, creating a map showing a smooth gradient of resilience across Chuuk. When examining individual reef types, the resilience scores were represented as circles and sized by their normalized values. All the maps were made using ArcGIS programming.

Last, the observed resilience scores were formally evaluated against the predicted scores using standard Pearson's correlation analyses. The observed resilience scores were also examined for their correlation with each individual metric used to predict resilience to gain a better understanding of the strengths and weaknesses of each metrics used to predict resilience.

Results

Benthic data collected prior to the 2016 temperature-induced bleaching disturbance revealed that reef types predicted significant variation in coral assemblages in this pre-disturbance state (PERMANOVA, Pseudo-F = 5.12, $P < 0.001$). Post-hoc comparisons revealed that most pairwise reef type comparisons were also significantly different from each other

(PERMANOVA, $t>1.5$, $P<0.001$) except for the patch/back and channel reefs (PERMANOVA, $t=1.48936$ $P = 0.024$) (Figure 5).

The bleaching event in 2016 caused mass mortality to Chuuk's reef corals, with negative impacts across most sites for all biological metrics. Yet, the magnitude of negative impacts differed. Negative changes in genus-growth richness occurred for outer, patch/back, and inner reefs, but a slight increase was noted for channel reefs that are influenced by currents and tides (Figure 6). Non-*Porites* corals and the benthic substrate ratio (BSR) decreased across all reef types, with greatest impacts to non-*Porites* corals (Figures 6-8). In order to understand the relative resistance and recovery for all metrics and reef types, percent changes were calculated from the raw data based upon differences between the first recorded value to the most recent in 2019 (Table 2). As expected, the overall percentage change was negative across all reef types for all three biological metrics, however, substantial variation existed. The percent change for genus-growth richness was less extreme compared with the percent change in BSR, and both were less extreme compared with the percentage change in non-*Porites* contribution. In addition, substantial site-level variation existed within each metric that was used to calculate resilience. However, prior to calculating resilience, this study described a process for dealing with a potential source of inherent natural variation associated with percentage change metrics.

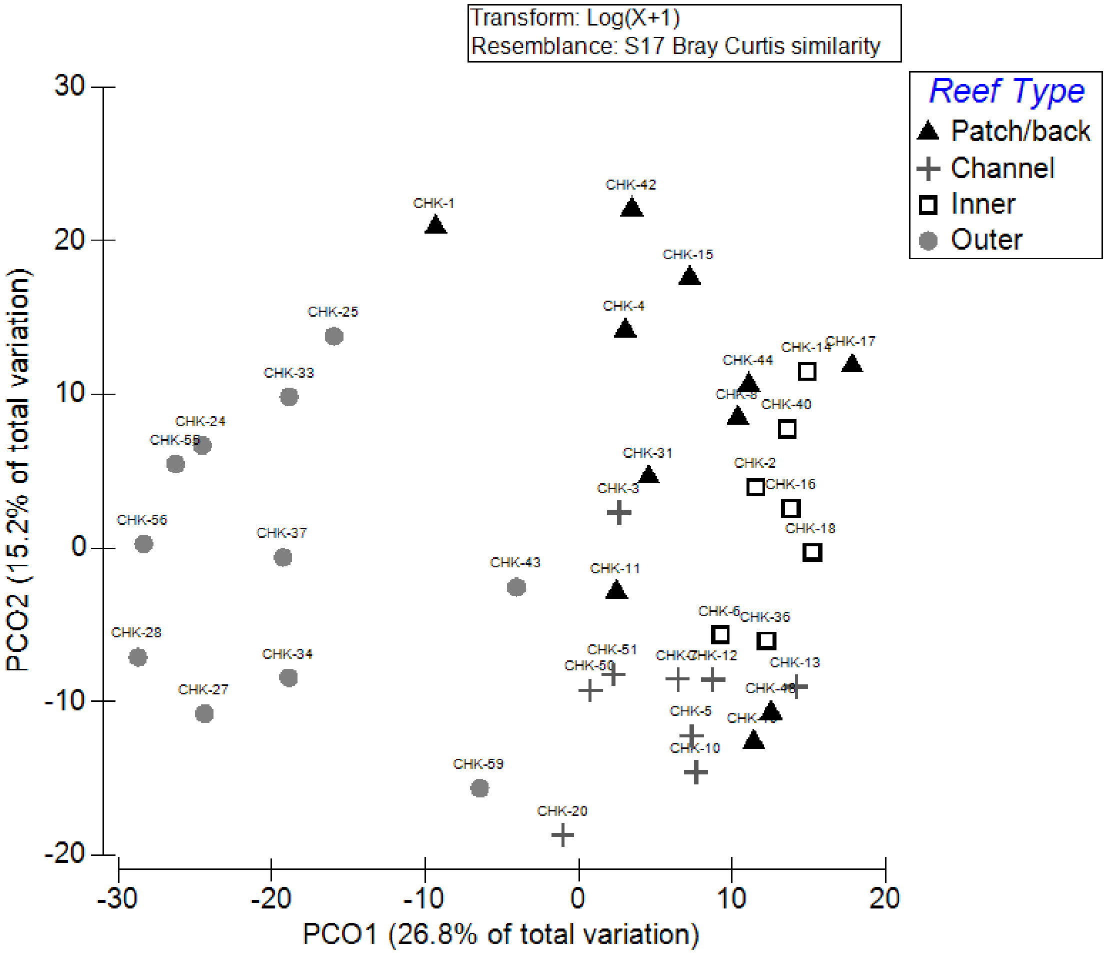


Figure 5: Principal coordinate ordination (PCO) of pre-disturbance benthic data from varying reef types across Chuuk.

Figure 6: Genus-growth richness for all study sites through each study year (2012−2019) with reef type color-coded. Empty bars indicate site was not visited that year.

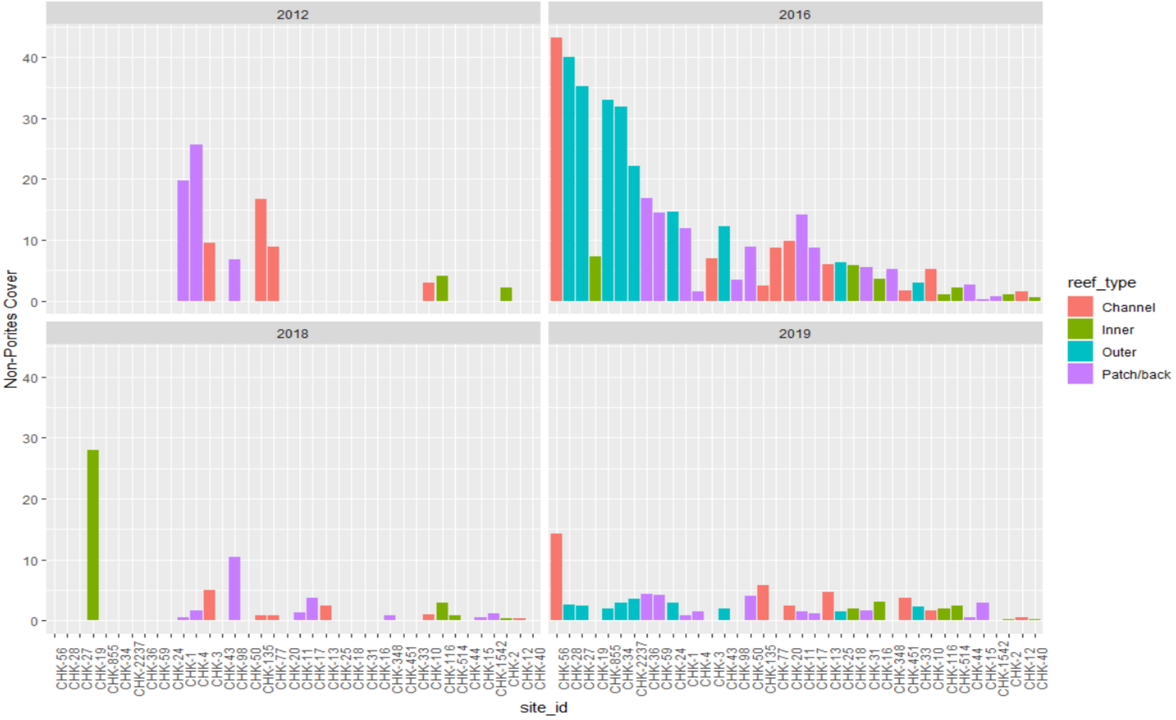


Figure 7: Non-*Porites* cover for all sites and years with reef type color-coded. Empty bars indicate site was not visited that year.

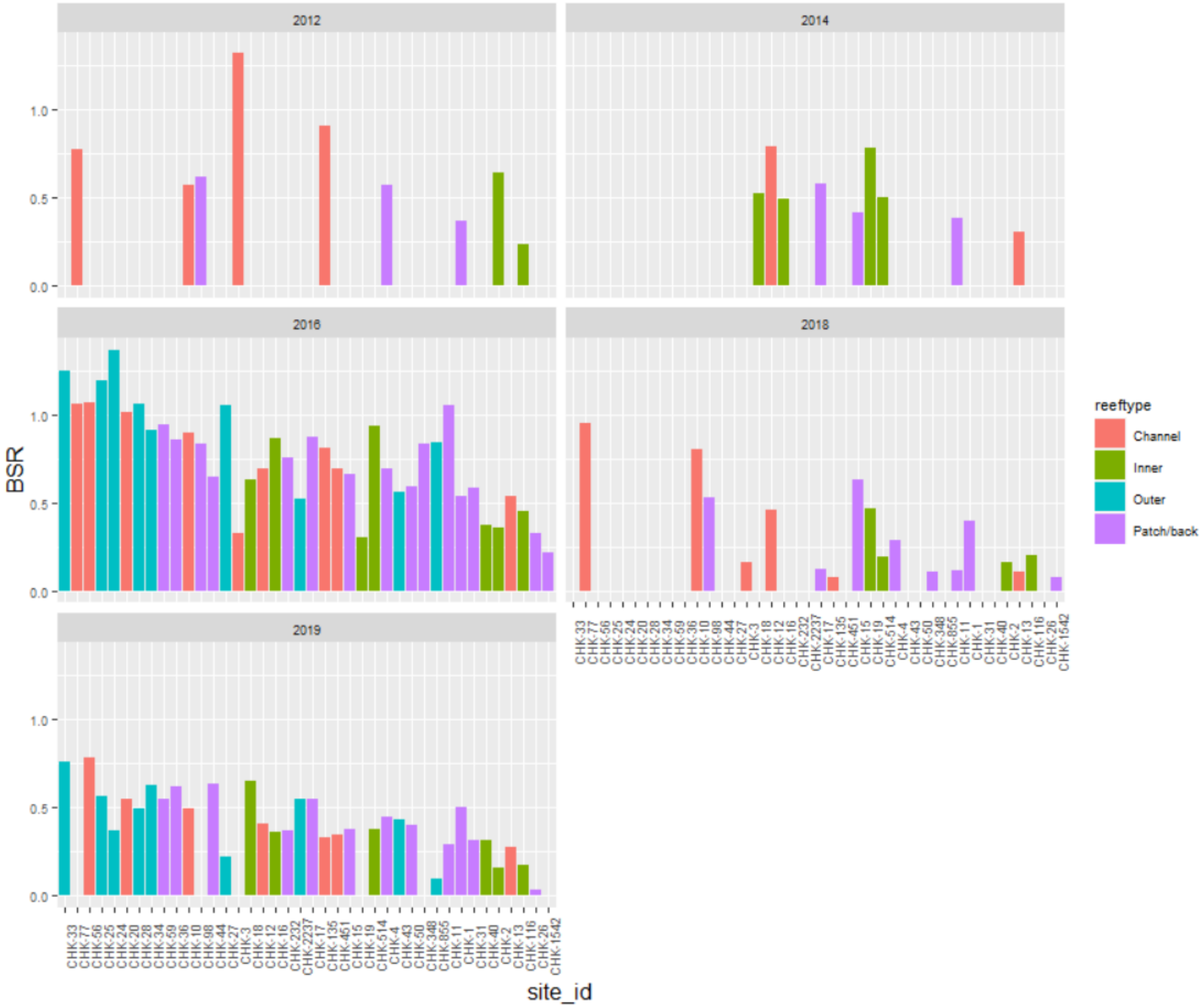


Figure 8: Benthic substrate ratio (BSR) values for all sites and years with reef type color-coded. Empty bars indicate site was not visited that year.

Table 2: Percent change in biological ‘condition’ metrics from earliest time point to most recent. Figures 6-8 for individual site earliest time point and most recent time point.

Study Sites		Biological Metric Data		
Site ID	Reef Type	Richness Percent Change	Non-*Porites* Contribution Percent Change	BSR Percent Change
CHK-12	channel	11.764706	-59.978712	-48.71111846
CHK-56	channel	8.695652	-66.907378	-26.82125217
CHK-20	channel	-3.703704	-75.109833	-46.39091687
CHK-13	channel	-5.555556	-22.258786	-10.60507062
CHK-135	channel	-11.111111	-65.266225	-63.45048249
CHK-77	channel	-25	-89.76525	22.66768874
CHK-10	channel	-39.130435	-44.103393	-13.77220402
CHK-451	channel	-40	118.214936	-50.46173163
CHK-3	channel	-46.666667	-47.974694	-87.50085646
CHK-16	inner	0	-14.948791	-27.25848929
CHK-40	inner	0	-72.849462	-16.62246196
CHK-514	inner	0	9.823322	-24.36442342
CHK-116	inner	-14.285714	-52.611068	-25.39886681
CHK-19	inner	-24.137931	285.190379	-41.07058715
CHK-98	inner	-25	53.916783	-13.9520521
CHK-2	inner	-58.333333	-89.607051	-74.83817141
CHK-18	inner	-58.823529	-64.558165	24.24458417
CHK-33	outer	40	-22.618125	-38.69007794
CHK-25	outer	11.111111	-76.202845	-52.82427897
CHK-24	outer	0	-80.042781	-73.06902057
CHK-2237	outer	-4	-83.599589	3.905702892
CHK-34	outer	-17.857143	-90.971949	-31.65602025
CHK-43	outer	-20.689655	-84.3107	-23.14785756
CHK-27	outer	-33.333333	-93.041191	-79.43230893
CHK-28	outer	-33.333333	-93.526312	-53.59307948
CHK-855	outer	-53.333333	-93.930154	-88.89060657
CHK-15	patch/back	100	1268.345324	-9.495731283
CHK-59	patch/back	7.407407	-70.284843	-41.75066398
CHK-348	patch/back	-5.882353	-83.380831	-87.37187011
CHK-1542	patch/back	-13.333333	65.877287	-66.41951674
CHK-50	patch/back	-20	-53.816289	-31.76964003
CHK-31	patch/back	-22.222222	-68.34243	-46.10841368
CHK-17	patch/back	-23.529412	-85.894117	-5.428253915
CHK-44	patch/back	-27.272727	-81.542461	-0.887804337
CHK-1	patch/back	-29.411765	-95.947021	34.36258454
CHK-11	patch/back	-29.411765	-89.350231	-23.49119554
CHK-4	patch/back	-43.478261	-93.902215	-21.78764313
CHK-36	patch/back	-48.387097	-73.903898	-28.4716289

Differing starting points in biological metrics, or differing initial biological status, were hypothesized to be influential predictors of the magnitude of change in some metrics and/or reef types. Because the variation in percentage change values may have been sensitive to initial states, it was desirable to remove this inherent source of variation that may have existed prior to determining resilience. Results from regression modeling that investigated the dependence of percentage change values on the starting states are described for all reef types grouped (i.e., island scale) and also for individual reef types prior to calculating resilience.

Island Scale Resilience

Regression modeling revealed a significant effect of the initial value (i.e., starting point) on percentage change for all three biological metrics, when all reef types were grouped for investigation at the island scale: genus-growth richness ($p= 0.04$, $R^2 = 0.1$), non-*Porites* contribution ($p=0.0005$, $R^2 = .28$), and BSR ($p=0.03$, $R^2 =0.13$) (Figure 9). Given this dependence, residuals were calculated for all metrics and used to calculate the observed resilience scores (Table 3). Resilience scores for each site were calculated using a Principal Component Analysis (PCA) (Table 4). Taking the scores of the first PCA axis explained 74% of the variation in the percent change values for all biological metrics (Figure 10). This yielded univariate observed resilience scores that were compared with predicted resilience scores from previous studies (Figure 11).

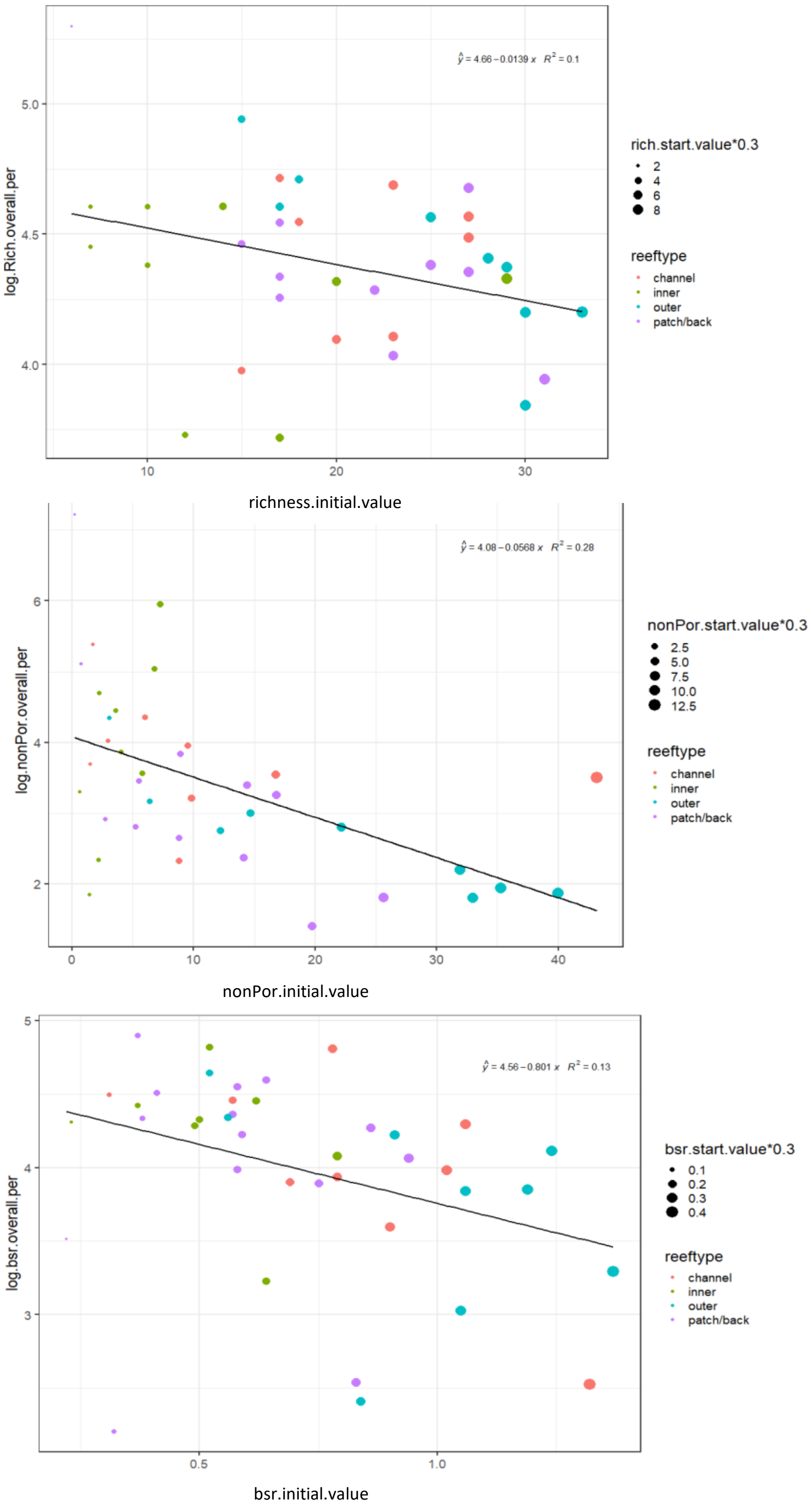


Figure 9: Log-transformed percentage change of biological metrics versus initial values in all study sites on the island scale. Reef type indicated by color for visual reference.

Table 3: Residuals derived from logistic regressions to be used in PCA for determining resilience scores.

	Island Scale Residuals to formulate PCA		
Site ID	**Richness**	**Non-Por**	**BSR**
CHK-1	-0.17	-1.56	0.64
CHK-10	-0.23	0.11	0.36
CHK-11	-0.17	-0.91	0.08
CHK-116	-0.11	0.01	-0.06
CHK-12	0.29	-0.30	0.01
CHK-13	0.14	0.62	0.18
CHK-135	0.20	0.42	-0.24
CHK-15	0.72	3.16	0.28
CHK-1542	0.01	1.08	-0.87
CHK-16	0.08	0.57	0.12
CHK-17	-0.09	-0.93	0.46
CHK-18	-0.71	-0.18	0.68
CHK-19	0.07	2.29	0.15
CHK-2	-0.77	-1.61	-0.82
CHK-20	0.28	-0.30	0.24
CHK-2237	0.25	-0.02	0.50
CHK-24	0.18	-0.25	-0.17
CHK-25	0.30	-0.55	0.25
CHK-27	-0.05	-0.13	-0.69
CHK-28	0.00	0.06	0.13
CHK-3	-0.48	0.42	-0.98
CHK-31	0.07	-0.31	-0.11
CHK-33	0.49	0.44	0.55
CHK-34	0.14	-0.06	0.40
CHK-348	0.12	-0.97	-1.36
CHK-36	-0.29	0.14	0.40
CHK-4	-0.31	-0.81	0.26
CHK-40	0.04	-0.74	0.16
CHK-43	0.11	-0.63	0.23
CHK-44	-0.07	-1.01	0.55
CHK-451	-0.29	1.41	-0.10
CHK-50	0.07	0.26	0.14
CHK-514	0.14	0.75	0.17
CHK-56	0.35	1.88	0.58
CHK-59	0.39	0.13	0.26
CHK-77	-0.07	-1.25	0.88
CHK-855	-0.40	-0.40	-1.48
CHK-98	-0.07	1.34	0.39

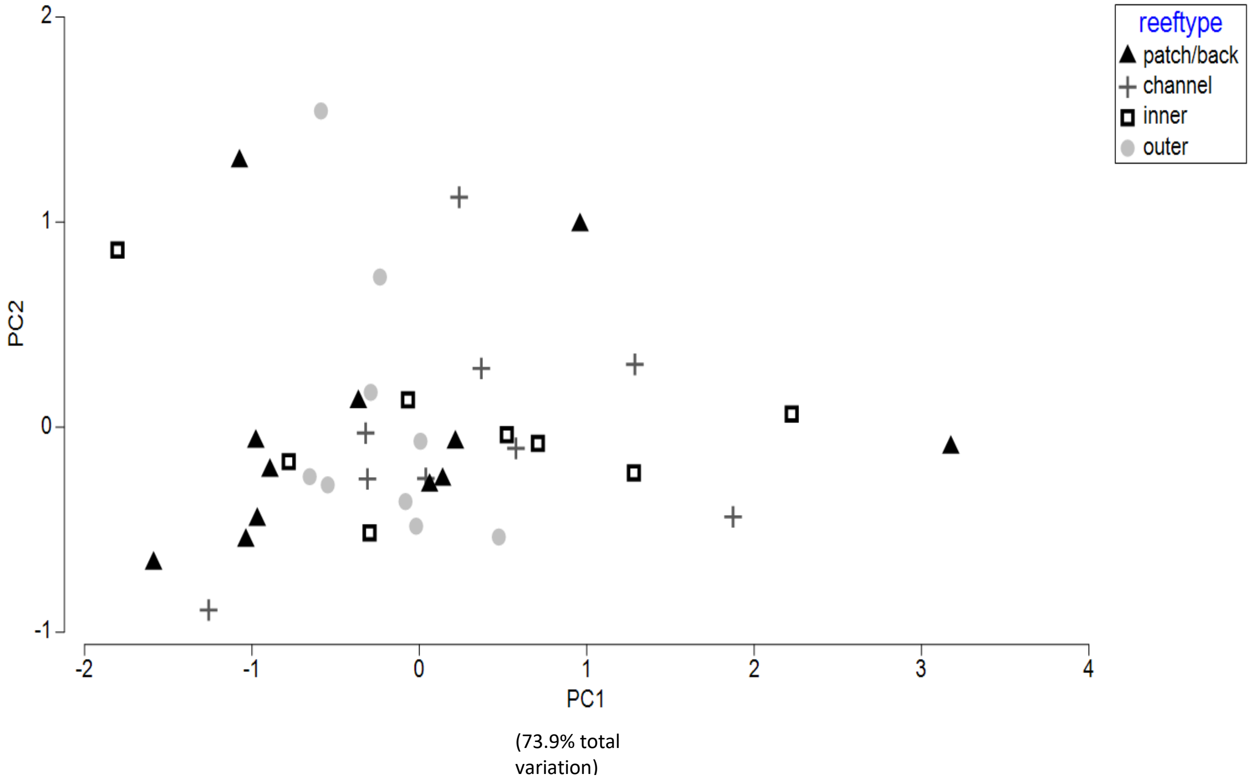


Figure 10: PCA analysis of sites on island scale using three biological metrics to a create singular resilience score from PC1 values.

Table 4: PC1 scores of Principal Component Analysis (PCA) used to represent resilience for island scale.

Study Sites	**Island Scale PCA Score (Resilience Score)**
Site ID	
CHK-1	-1.59
CHK-10	0.0389
CHK-11	-0.977
CHK-116	-0.068
CHK-12	-0.321
CHK-13	0.577
CHK-135	0.371
CHK-15	3.18
CHK-1542	0.96
CHK-16	0.523
CHK-17	-0.968
CHK-18	-0.297
CHK-19	2.22
CHK-2	-1.8
CHK-20	-0.31
CHK-2237	-0.019
CHK-24	-0.291
CHK-25	-0.547
CHK-27	-0.236
CHK-28	0.00659
CHK-3	0.238
CHK-31	-0.364
CHK-33	0.475
CHK-34	-0.0825
CHK-348	-1.07
CHK-36	0.0613
CHK-4	-0.893
CHK-40	-0.78
CHK-43	-0.655
CHK-44	-1.04
CHK-451	1.29
CHK-50	0.215
CHK-514	0.708
CHK-56	1.87
CHK-59	0.139
CHK-77	-1.26
CHK-855	*-0.588*
CHK-98	1.28

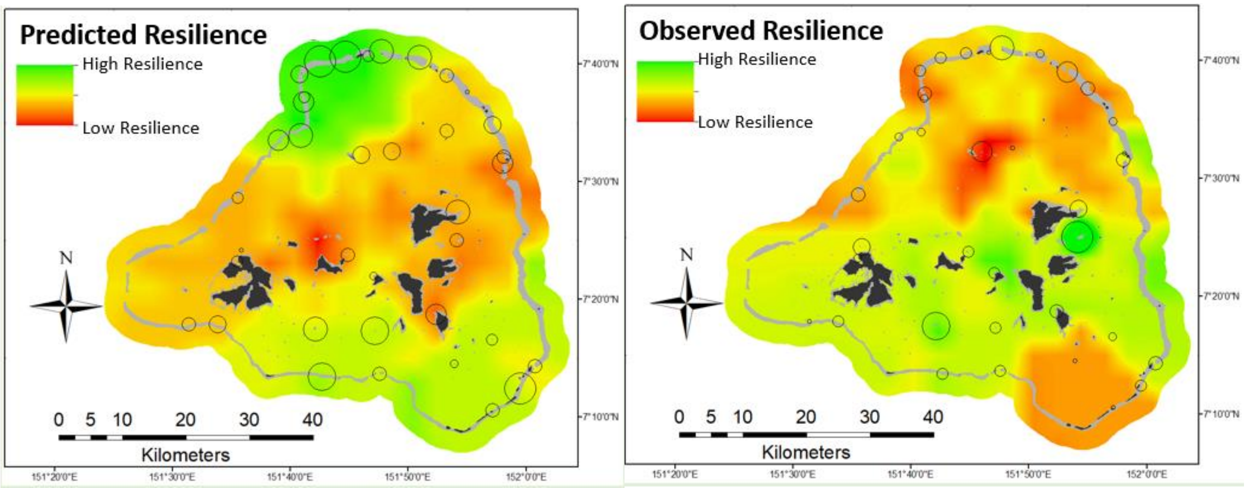


Figure 11: Kriging (spatial autocorrelation) maps of observed resilience vs. predicted resilience.

Green indicates high resilience; red indicates low resilience

For most study sites, observed resilience scores differed significantly from the predictions of the 2016 rapid assessment study. Interestingly, this comparison revealed that areas with a high predicted resilience often had a low observed resilience. In addition, reefs with low predicted resilience had a high observed resilience (Figure 11). In support, the correlation between predicted (2016 snapshot study) versus observed resilience (the present study) was not significant (R^2=0.032) (Figure 12).

Predicted versus observed resilience within reef type

When examining regressions within each reef type, similar dependencies on initial values were less prevalent for all biological metrics than seen on the island scale assessment. Regressions for genus-growth richness revealed significant negative relationships between initial values and overall percentage change for outer (p=0.003, R^2 = 0.73, Figure 13) and patch/back reefs (p=0.019, R^2 =0.43, Figure 13). Non-*Porites* contribution showed significant negative relationship with percentage change in outer (p<0.001, R^2 = 0.83, Figure 14), inner (p= 0.031, R^2 = 0.5, Figure 14), and patch/back reefs (p=0.01, R^2 =.498, Figure 14). BSR showed a significant negative relationship at channel reefs (p= 0.039, R^2 = 0.48, Figure 15). Residuals were calculated for all significant relationships, while raw values were used for non-significant relationships, and together built the observed resilience scores (Table 5). Values for each metric were similarly used for a Principal Component Analyses that combined the biological metrics to generate a single score for each reef type (Figure 13-15, Table 5). Resilience scores for each site were derived from PC1 scores of a Principal Component Analysis (PCA) conducted separately for each reef type (Figure 16). This created a singular resilience score from the multiple metric values (Table 6).

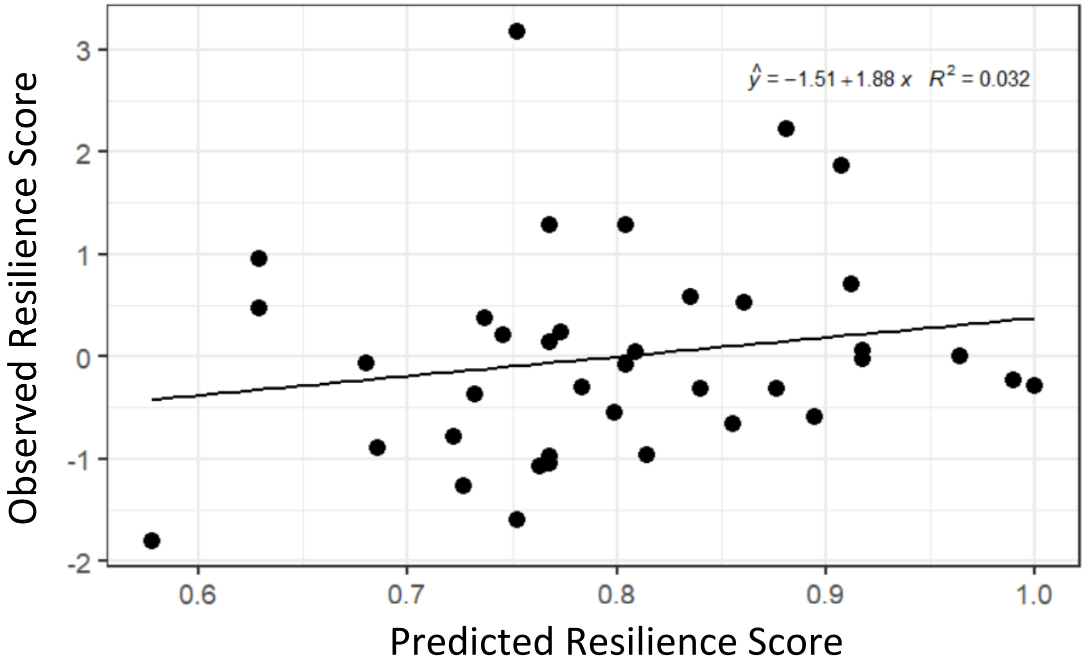


Figure 12: Relationship between observed resilience versus predicted resilience.

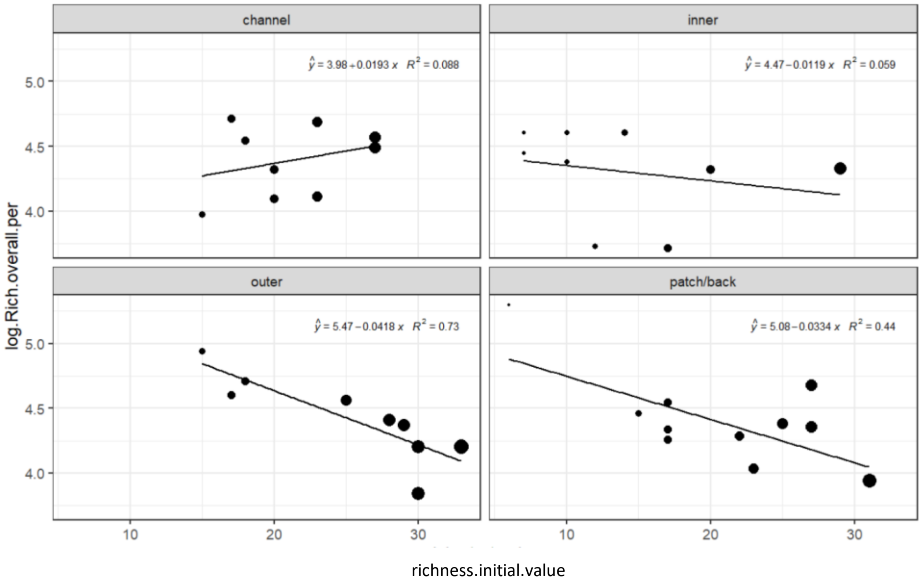


Figure 13: Regression analyses depicting the relationship between the initial value of genus-growth richness versus the overall change value (log transformed percent change).

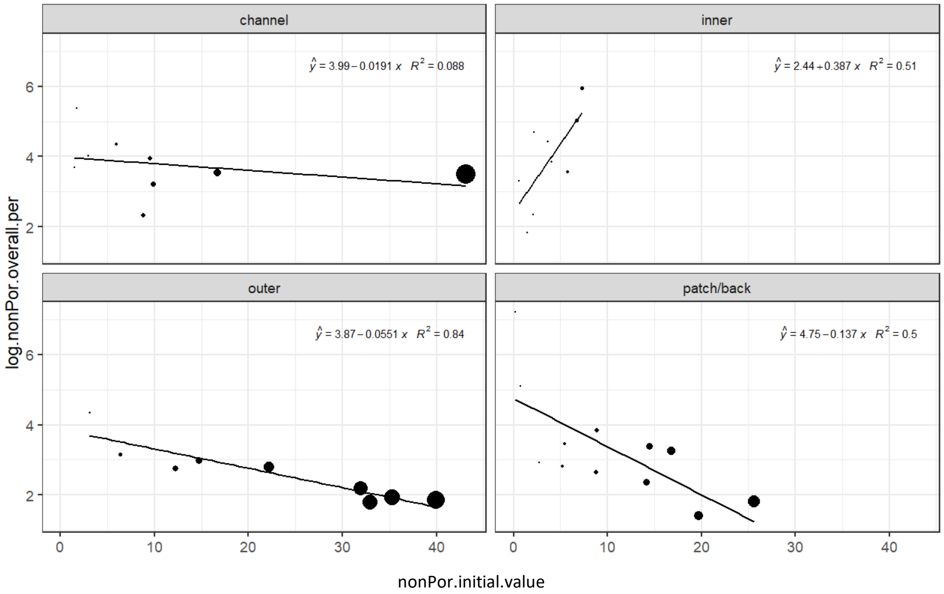


Figure 14: Regression analyses depicting the relationship between the initial values of Non-*Porites* contribution versus the overall change value (log-transformed percent change).

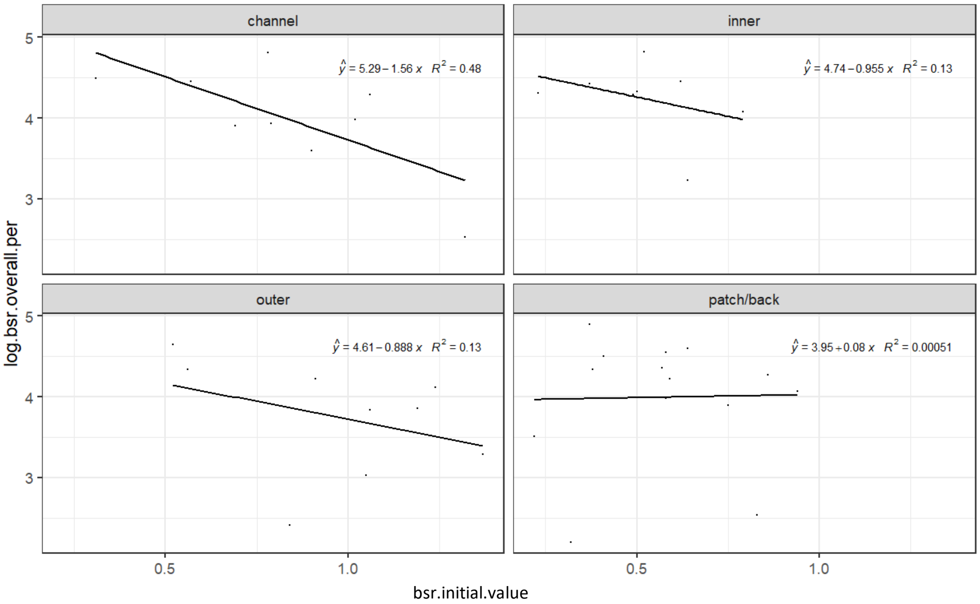


Figure 15: Regression analyses depicting the relationship between the initial of benthic substrate ration (BSR) versus the overall change value (log transformed percent change).

Table 5: PC1 scores of Principal Component Analysis (PCA) used to represent resilience for reef type scale

		Reef Type Normalized values for PCA		
		*Red indicates use of residual		
Site ID	**Reef Type**	**Richness**	**Non-*Porites***	**BSR**
CHK-1	patch/back	-0.25709	-0.6470866	4.900542
CHK-10	channel	4.108733	4.023504	0.05634442
CHK-11	patch/back	-0.25709	-0.451315	4.337406
CHK-116	inner	4.45102	-0.13941906	4.312156
CHK-12	channel	4.716396	3.689412	-0.11963828
CHK-13	channel	4.548012	4.353386	-0.31358116
CHK-135	channel	4.487387	3.547713	-0.28667635
CHK-15	patch/back	0.417433	2.4964384	4.505397
CHK-1542	patch/back	-0.1186	0.4564557	3.513945
CHK-16	inner	4.60517	0.61065206	4.286912
CHK-17	patch/back	-0.17705	-0.9016883	4.549359
CHK-18	inner	3.717867	-1.10990761	4.822252
CHK-19	inner	4.328917	0.69665031	4.07634
CHK-2	inner	3.729701	-0.92374838	3.225328
CHK-20	channel	4.56743	3.214473	0.28375739
CHK-2237	outer	0.137019	0.15095633	4.643484
CHK-24	outer	-0.15628	-0.06548871	3.293277
CHK-25	outer	-0.00915	-0.34918462	3.853879
CHK-27	outer	-0.0188	0.01393221	3.023721
CHK-28	outer	0.106497	0.20097365	3.837449
CHK-3	channel	3.976562	3.95173	-0.70384297
CHK-31	patch/back	0.17347	-0.5499332	3.986974
CHK-33	outer	0.096662	0.64760586	4.115942
CHK-34	outer	0.106426	0.09134466	4.224553
CHK-348	patch/back	0.030589	-1.2261315	2.535927
CHK-36	patch/back	-0.10319	0.8115081	4.270094
CHK-4	patch/back	-0.27919	0.5649872	4.359428
CHK-40	inner	4.60517	0.63862633	4.423379
CHK-43	outer	0.1131	-0.4424214	4.341883
CHK-44	patch/back	-0.06045	-1.4664619	4.596252
CHK-451	channel	4.094345	5.385481	-0.31051949
CHK-50	patch/back	0.134927	0.2985661	4.22289
CHK-514	inner	4.60517	1.40144248	4.325927
CHK-56	channel	4.688552	3.49931	0.657405
CHK-59	patch/back	0.496244	0.6146609	4.064733
CHK-77	channel	4.317488	2.325789	0.73675144
CHK-855	outer	-0.37547	-0.24771798	2.40779
CHK-98	inner	4.317488	-0.01774234	4.454905

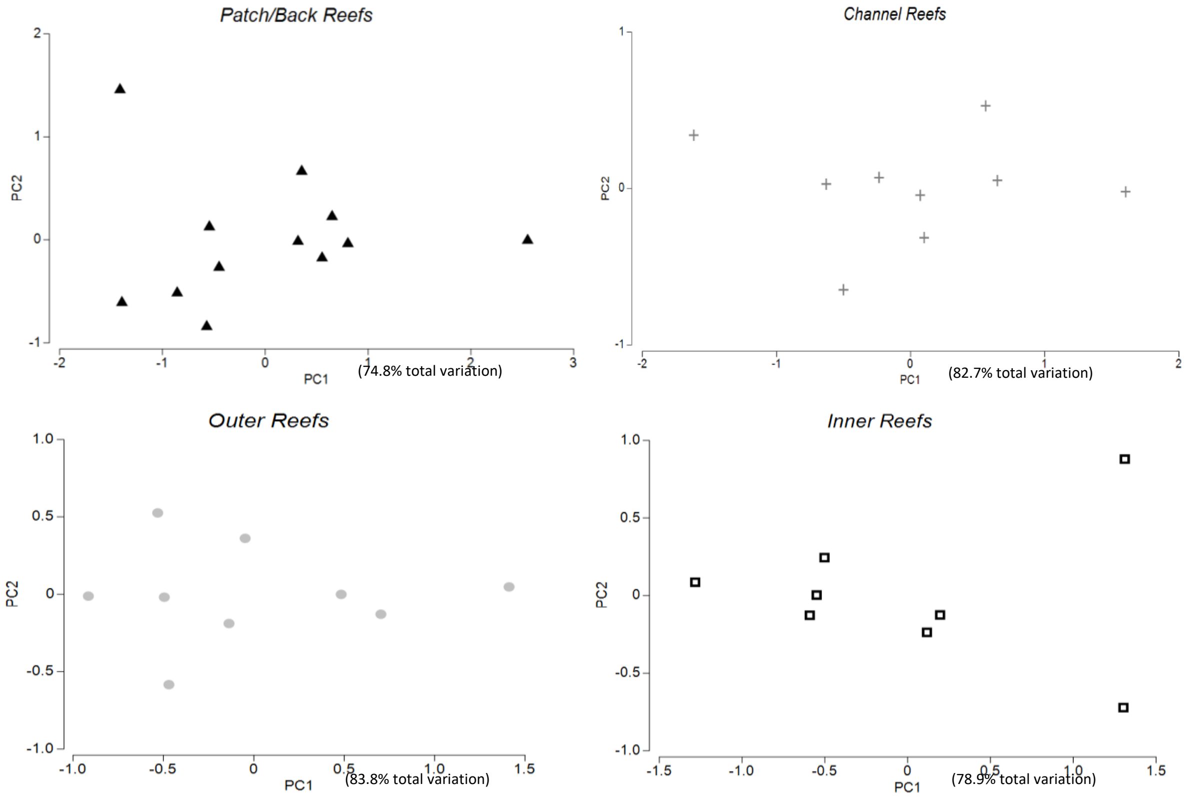


Figure 16: Principal Component Analysis (PCA) of each reef type using 3 biological metrics to create singular resilience score from PC1 values.

Table 6: PC1 scores of Principal Component Analysis used to represent resilience reef type-normalized scale.

Study Sites		**Reef Type PCA Score (Resilience Score)**
Site ID	**Reef Type**	
CHK-10	channel	-0.235
CHK-12	channel	0.0714
CHK-13	channel	-0.629
CHK-135	channel	0.101
CHK-20	channel	0.647
CHK-3	channel	-0.501
CHK-451	channel	-1.62
CHK-56	channel	0.56
CHK-77	channel	1.6
CHK-116	inner	0.196
CHK-16	inner	-0.55
CHK-18	inner	1.3
CHK-19	inner	-0.502
CHK-2	inner	1.31
CHK-40	inner	-0.591
CHK-514	inner	-1.28
CHK-98	inner	0.117
CHK-2237	outer	-0.915
CHK-24	outer	0.483
CHK-25	outer	-0.0481
CHK-27	outer	0.703
CHK-28	outer	-0.137
CHK-33	outer	-0.47
CHK-34	outer	-0.495
CHK-43	outer	-0.532
CHK-855	outer	1.41
CHK-1	patch/back	-0.57
CHK-11	patch/back	-0.45
CHK-15	patch/back	2.55
CHK-1542	patch/back	0.354
CHK-17	patch/back	-0.857
CHK-31	patch/back	-0.544
CHK-348	patch/back	-1.41
CHK-36	patch/back	0.803
CHK-4	patch/back	0.552
CHK-44	patch/back	-1.39
CHK-50	patch/back	0.318
CHK-59	patch/back	0.649

For most study sites, resilience scores for each reef type differed from the predictions of the 2016 rapid assessment study (Figure 17). This was particularly evident for inner reefs which were predicted to have lower resilience but showed high resilience in this study. As a last step, the predicted and calculated scores were normalized by reef type to remove differences in scaling and draw improved site-by-site comparisons. Most inner reef sites had a higher observed resilience compared with their predicted resilience, whereas most outer reef sites had a lower observed resilience compared with their observed resilience. Both patch/back and channel reef types had sites with mixed responses that were higher and lower than their predicted resilience.

Correlation of individual resilience components

Interestingly, calculated resilience scores correlated well with some individual metrics used in the 2016 rapid-assessment study to predict resilience (Figure 18). However, few consistent patterns were evident across habitats. All reef types showed a negative correlation to physical characteristics of reefs (i.e., a metric combining rugosity, slope, and mixing). Growth margin and disease were strongly correlated in three of the four reef types. Channel and outer reefs showed correlations with similar metrics, but these correlations were contrasting. Finally, coral recovery metrics (regrowth, reorientation, and recruits) did not reveal strong correlations (Figure 18).

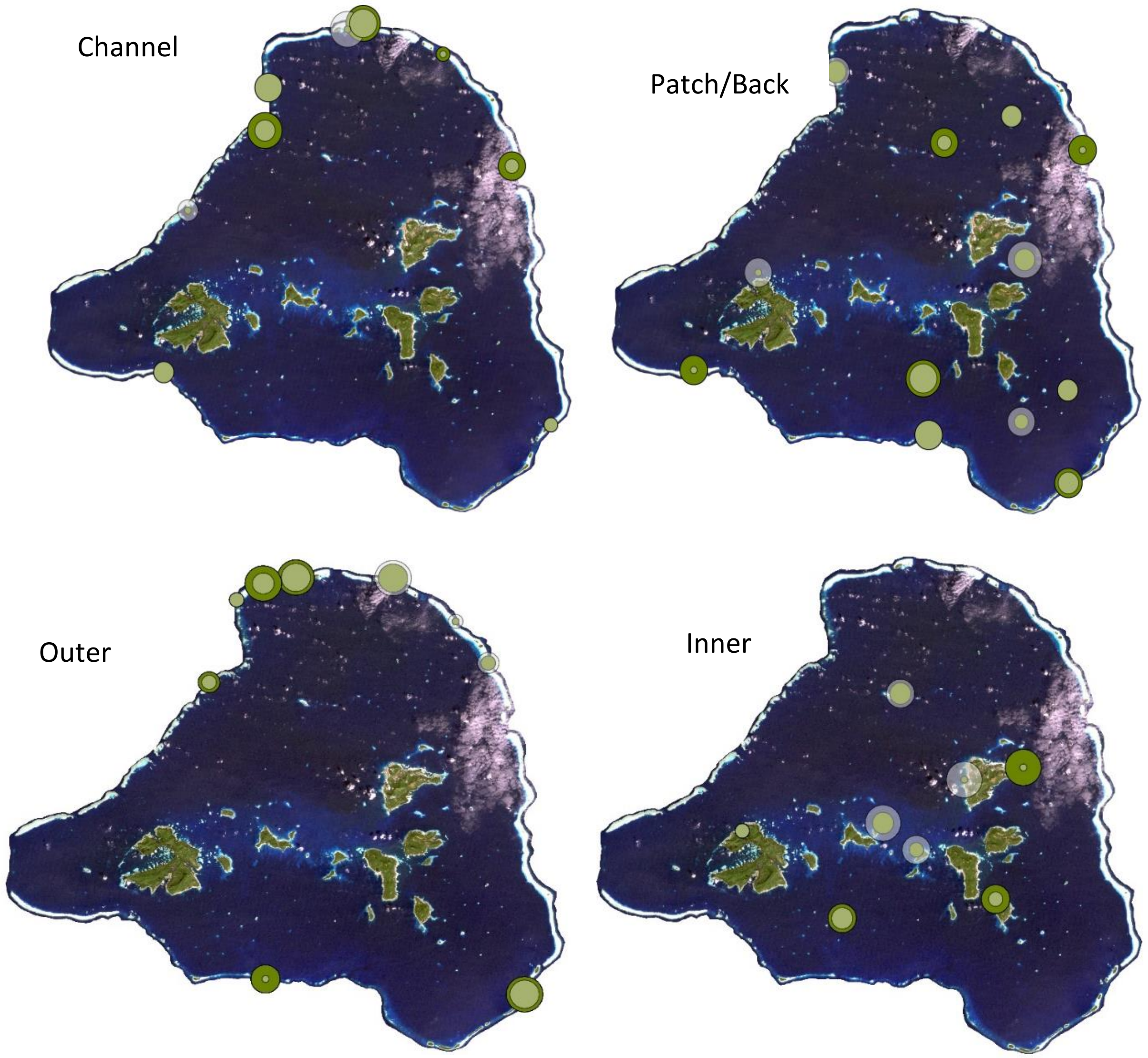


Figure 17: Comparison of predicted versus observed resilience for all study sites, organized by reef type. Dark green circles represent 2016 resilience score while white/opaque circles represent observed resilience from this study. Larger circles show higher resilience.

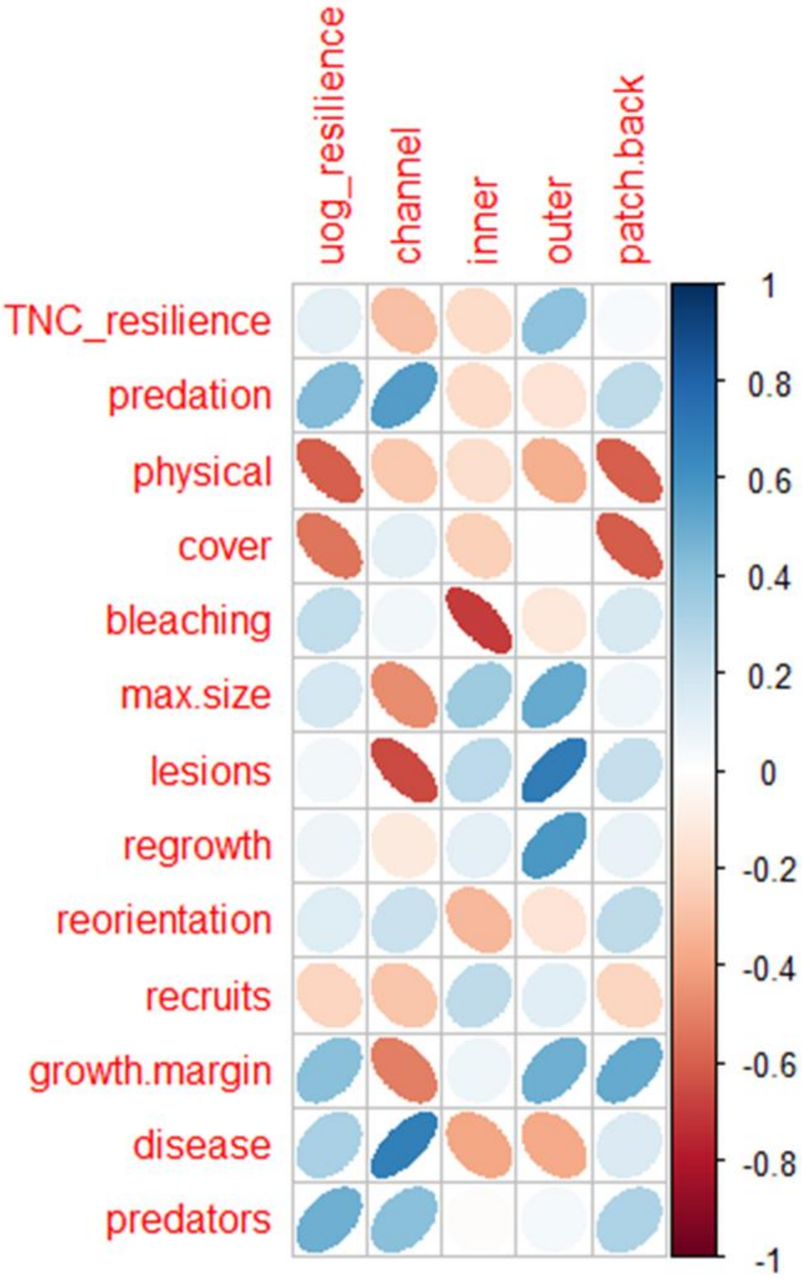


Figure 18: Correlations between predicted and observed resilience scores against TNC rapid assessment metrics. Blue represents positive correlations; red represents negative. Intensity of color demonstrates the strength of the correlations. Ellipse eccentricity scaled to correlation strength.

Discussion

Resilience Trends

The most dramatic result of the present study was the contrasting spatial maps depicting nearly opposite patterns in the predicted resilience from the 2016 rapid assessment versus the observed resilience from longer-term monitoring. To potentially explain these contrasting results, it is necessary to break down the definition of resilience and re-examine the sampling designs. Resilience is *the ability of a system to withstand and/or recover from a disturbance to maintain its functional state through time* (West and Salm 2003, Holling 1973, Bellwood et al. 2004, Nystrom and Folke 2000). Long-term data revealed that inner and patch reefs closest to the largest islands with known human impacts from watersheds and fishing remained the most stable through time. These reefs were *Porites* dominated, and therefore were less likely to have their coral populations affected by a bleaching event (Pratchett et al. 2013, Reynolds 2016). As a result, these reefs had the highest observed resilience scores, and are expected to remain relatively stable through time given their location in sheltered, productive environments with varying exposure to human disturbances. In summary, these inner reefs may have been *Porites* dominated for long time periods due to natural and/or anthropogenic causes that led to their stability across the 2016 disturbance event.

However, resilient reefs are often assumed to support diverse coral assemblages with high coral cover and favorable substrate for recruitment, indicating a “healthy” and functioning system. This study revealed that such a “preconceived healthy” reef system does not necessarily mean that the system is able to resist disturbance events. Instead, we confirmed that disturbance impacts are likely magnified for these “healthy” reefs as initial conditions often predicted a significant portion of the variance describing disturbance impacts (Allison 2004, Pfisterer and

Schmid 2002). One explanation could be that systems with high coral cover are more likely to have genetic clones (i.e., genets) that will be lost in a disturbance (Ayre and Hughes 2004, Hubbell 1997). A second mechanism could be that high species richness at some study sites disproportionally supported sensitive *Acropora* coral species compared with tolerant, *Porites* corals at sites with low species richness (Allison 2004). Though the mechanisms are not clearly understood, the concept of 'have-more, lose-more' was confirmed in our study. This phenomenon led to inner and patch reefs, closest to land, changing the least through the thermal-stress disturbance. Therefore, accounting for reef type is one clear means to address some of the bias in rapid-assessment studies of resilience.

The present study subsequently stratified the field data by reef type to better understand relationships between observed and predicted resilience. Despite stratification, relationships between predicted and observed resilience remained weak with unclear patterns potentially associated with several factors. First, prior to the major disturbance, reefs with and without significant localized stressors, in our case high fishing pressure (Cuetos-Bueno et al. 2018), may similarly be in high-coral-cover states. These sites would score similarly high for resilience before disturbance because of the present state of the coral assemblages. However, if a disturbance causes a loss in corals, and some reefs heavily exploited with less herbivorous fish to crop algae and promote recovery, then differential recovery will be observed. This was classically defined as the 'Paradox of Enrichment'; ecological stability thresholds get crossed but no changes in the ecological states are evident until a disturbance event (Rosenzweig 1971).

Second, the lack of any clear relationship between predicted and observed resilience may, in part, be an artifact of the resilience scoring process. Resilience studies are diverse and use between 10 and 60 metrics that depict the physical, environmental, and biological factors into a singular score (McClanahan et al. 2012, West and Salm 2003). Physical and environmental aspects of a reef, such as wave exposure, currents, and turbidity, can vary by time, day, and season. Rapid assessments collecting these metrics record a temporary state of a reef, which may not be representative throughout time. By contrast, biological indicators will typically be more stable across these dynamic environmental patterns. Therefore, combining variable environmental metrics with stable biological metrics may lead to inconsistencies between long-term data and rapid-assessment studies.

Third, rapid-assessment studies typically weight environmental indicators equally when scoring resilience. However, studies have shown that certain environmental factors have more influence on 'condition' than others, often forming a hierarchical set of response (Houk et al. 2015, Maynard, 2010 McLean 2016). Logically, this becomes more problematic as the number of metrics increases, as the law of averages takes greater precedence.

Fourth, as seen in select sites in this study, individual reefs with unique characteristics and 'conditions' create other disparities measuring resilience. For example, channel site CHK-135 has been exposed to extensive dynamite fishing. Therefore, there is little coral structure remaining. However, fish populations are high in this area at every trophic level. The low coral cover would drive down the resilience score, though the reef would be free of algal substrate and may recover rapidly to a coral-dominated state now that enforcement has curbed dynamite fishing. However, by weighting all metrics equally, these unique situations get merged. A different example, CHK-2 is located adjacent to the main island of Weno and is chronically exposed to high pollution levels, creating a *Porites*-dominated reef that is resilient to additional stress. Acute disturbances have less effect on this site due to its already tolerant state.

Long-term reef trends

The present findings were dependent upon the three biological metrics selected for determining long-term trends. These trends build upon each other sequentially to define the temporal response to disturbance events; beneficial substrates can lead to the recruitment of new species, and eventually coral growth occurs. However, further work is needed to understand the sensitivities associated with metrics of long-term trends.

This study found that all three biological metrics were sensitive to disturbance. Richness, non-*Porites* contribution, and the benthic substrate ratio of calcareous to non-calcareous substrate declined following the bleaching event in 2016. The responsiveness of these metrics indicates their suitability for assessing various aspects of resilience. In the years following disturbances, richness and increased substrate ratios are expected to increase while new corals settle and grow. Therefore, tracking richness and substrate ratios provides an indication of recovery potential that could be examined spatially. Non-*Porites* cover provided an indication of how sensitive corals responded to heat stress, and thus could be used to examine resistance spatially. Together, these metrics aimed to capture both resistance and recovery from the long-term data. Capturing aspects of resilience studies that best aligned with these trends was ideal to improve our recommendations for resilience studies.

Yet, in order to bolster management portfolios to mitigate climate disturbances, further studies are needed to understand and prioritize the local factors driving both long-term trends and/or resilience snapshots. Therefore, isolating biological metrics that match long-term trends is recommended to improve resilience predictions. Additionally, understanding the relationships between local stressors (such as pollution or overfishing), natural influences (such as wave regimes or physical structure), and resilience predictions could provide better guidance for management location and policy. This has been similarly suggested in a recent study by Bang et al. (2021) where some indicators were influential to resilience measurements only at particular locations whereas other ‘indicators’ of resilience influenced predictions to veer away from post disturbance observations. This further emphasizes the importance of selecting a few, powerful indicators while incorporating specific local influences to best predict resilience (Bang et al. 2021). In conclusion, future studies should seek to narrow down resilience factors to the most influential biological indicators, determine relationships between localized factors and ‘condition’, and utilize long-term monitoring to make more effective resilience predictions.

Conclusions

The observed resilience across a disturbance event on reefs in Chuuk, FSM, did not correlate with predicted resilience reported by a 2016 rapid-assessment study. This suggests that rapid-assessment studies many not be able to predict reef resilience. A number of unintended biases in rapid-assessment studies may be able to explain this difference, such as weighting all metrics equally, combining biological, physical, and environmental indicators into a singular score, or not stratifying by habitats. Additionally, this study calls into the question the very definition of resilience by demonstrating that reef health, resistance, and recovery are not synonymous and that reefs often do not express all these aspects of resilience. Therefore, it is critical to define clear research goals when investigating reef ‘condition’ and attempting to predict future states.

This study demonstrated that current methods of rapid-assessment studies of resilience are not able to depict actual reef processes through disturbance events and that rapid studies are too sensitive to fluctuations in environmental conditions. However, rapid-assessment studies are still very valuable to coral reef conservations and the present study offers some guidelines to improve such studies, including prioritizing local factors influencing reef “condition” and stratifying by habitat type. Long-term monitoring data and resilience studies could be combined to identify thresholds and predictions, respectively, beyond which undesirable changes will likely occur. This would facilitate proactive management, especially if recorded over long periods of time.

To thoroughly examine resilience, it would be beneficial to conduct a similar but longer study. Because of the relatively short-term nature of the data, it most likely did not capture the reefs’ recovery potential, which could affect resilience scores and future resilience potential. While Chuuk allowed for the examination of four different habitat types it would be beneficial to conduct this study across the entire region of Micronesia where disturbance histories are varied. Similarly, this study was only compared against a single rapid assessment study. It would be ideal to analyze other islands and regions against varying rapid assessment studies to identify if any predictive resilience strategies or metrics are more effective than others.

Reef resilience has become a popular and important topic in coral reef ecology. However, scientists do not have a clear understanding on what it means for a reef to be resilient or how to best predict which reefs will be resilient. Reconciling these problems is critical to prioritize management efforts and maximize efficiency in conserving our coral reef ecosystems.

References

Alvarez-Filip, L., J. P. Carricart-Ganivet, G. Horta-Puga, and R. Iglesias-Prieto. 2013. Shifts in coral-assemblage composition do not ensure persistence of reef functionality. *Scientific Reports* 3:1–5.

Aronson, R. B., and W. F. Precht. 1997. Stasis, biological disturbance, and community structure of a Holocene coral reef. *Paleobiology* 23:326–346.

Arye, D., & Hughes, T. P. (2004). Climate change , genotypic diversity and gene flow in reef-building corals. *Ecology Letters*, 7, 273–278.

Bang, A. H. Y., Kuo, C., Wen, C. K., & Cherh, K. (2021). Quantifying Coral Reef Resilience to Climate Change and Human Development : An Evaluation of Multiple Empirical Frameworks. *Frontiers in Marine Science,* 7(January), 1–12.

Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nyström. 2004. Confronting the coral reef crisis. *Nature,* 429:827–33.

Berumen, M. L., and M. S. Pratchett. 2006. Recovery without resilience: Persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea. *Coral Reefs,* 25:647–653.

Birrell, C. L., L. J. McCook, and B. L. Willis. 2005. Effects of algal turfs and sediment on coral settlement. *Marine Pollution Bulletin,* 51:408–414.

Bozec, Y. M., and P. J. Mumby. 2015. Synergistic impacts of global warming osn the resilience of coral reefs. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 370:1–9.

Chollett, I., and P. J. Mumby. 2012. Predicting the distribution of Montastraea reefs using wave exposure. *Coral Reefs,* 31:493–503.

Cinner, J. E., C. Huchery, E. S. Darling, A. T. Humphries, N. A. J. Graham, C. C. Hicks, N. Marshall, and T. R. McClanahan. 2013. Evaluating social and ecological vulnerability of coral reef fisheries to climate change. *PloS One,* 8.

Clarke, K. R., & Gorley, R. N. (2015). Primer: User manual/tutorial. Primer-E Ltd., Plymouth, UK, 93.

Cuetos-bueno, J. 2012. Advancing the Micronesia Challenge through Community-Based Management of Marine Resources in Piis-Paneu, Chuuk Final Report.

Donovan, M. K., A. M. Friedlander, J. Lecky, J. B. Jouffray, G. J. Williams, L. M. Wedding, L. B. Crowder, A. L. Erickson, N. A. J. Graham, J. M. Gove, C. V. Kappel, K. Karr, J. N. Kittinger, A. V. Norström, M. Nyström, K. L. L. Oleson, K. A. Stamoulis, C. White, I. D. Williams, and K. A. Selkoe. 2018. Combining fish and benthic communities into multiple regimes reveals complex reef dynamics. *Scientific Reports*, 8:1–11.

Gouezo, M., Y. Golbuu, K. Fabricius, D. Olsudong, G. Mereb, V. Nestor, E. Wolanski, P. Harrison, C. Doropoulos, E. Wolanski, P. Harrison, and C. Doropoulos. 2019. Drivers of recovery and reassembly of coral reef communities. *Proceedings of the Royal Society B: Biological Sciences*, 286.

Graham, N. A. J., S. Jennings, M. A. MacNeil, D. Mouillot, and S. K. Wilson. 2015. Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature*, 518:94–97.

Green, A. L., and D. R. Bellwood. 2009. Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience - A practical guide for coral reef managers in the Asia Pacific region. *IUCN working group on Climate Change and Coral Reefs*, 7

Heenan, A., and I. D. Williams. 2013. Monitoring herbivorous fishes as indicators of coral reef resilience in American Samoa. *PLoS ONE*, 8.

Heyward, A. J., and A. P. Negri. 1999. Natural inducers for coral larval metamorphosis. *Coral Reefs*, 18:273–279.

Hoegh-Guldberg, O., J. Mumby, J. Hooten, S. Steneck, P. Greenfield, E. Gomes, D. Harvell, F. Sale, J. Edwards, K. Caldeira, N. Knowlton, M. Eakin, R. Iglesias-Prieto, N. Muthiga, H. Bradbury, A. Dubi, and E. Hatziolos. 2007. Coral reefs under rapid climate change and ocean acidification. *Science*, 318:1737.

Holling, C. S. 1973. Resilience and Stability. *Annual Review Ecological System*, 4:1–23.

Houk, P., D. Benavente, and V. Fread. 2011. Characterization and evaluation of coral reefs around Yap Proper, Federated States of Micronesia. *Biodiversity and Conservation,* 21:2045–2059.

Houk, P., D. Benavente, J. Iguel, S. Johnson, and R. Okano. 2014. Coral Reef Disturbance and Recovery Dynamics Differ across Gradients of Localized Stressors in the Mariana Islands. *PLoS ONE,* 9:e105731.

Houk, P., R. Camacho, S. Johnson, M. Mclean, S. Maxin, J. Anson, E. Joseph, O. Nedlic, M. Luckymis, K. Adams, D. Hess, E. Kabua, A. Yalon, E. Buthung, and C. Graham. 2015. The Micronesia Challenge : Assessing the Relative Contribution of Stressors on Coral Reefs to Facilitate Science-to-Management Feedback. *PLoS ONE*,1–17.

Houk, P., J. Deblieck, D. Benavente, S. Maxin, A. Yalon, M. Mclean, C. Teresio, C. Graham, S. Kutta, J. Cuetos-Bueno, L. Stephen, and T. Leberer. 2016. Status and management of coral reefs and fisheries resources in Chuuk Lagoon and Kuop Atoll , Federated States of Micronesia. *Technical report prepared for The Nature Conservancy and the US Department of Interior*.

Houk, P., and R. Van Woesik. 2010. Coral assemblages and reef growth in the Commonwealth of the Northern Mariana Islands (Western Pacific Ocean). *Marine Ecology,* 31:318–329.

Houk, P., Yalon, A., Maxin, S., Starsinic, C., Mcinnis, A., Gouezo, M.,… Woesik, R. Van. (2020). Predicting coral-reef futures from El Niño and Pacific Decadal Oscillation events. *Scientific Reports*, 1–9.

Hughes, T. P., and J. H. Connell. 1999. Multiple stressors on coral reefs : A long-term perspective. *American Society of Limnology and Oceangraphy,* 44:932–940.

Hughes, T. P., A. H. Baird, D. R. Bellwood, M. Card, S. R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J. B. C. Jackson, J. Kleypas, J. M. Lough, P. Marshall, M. Nyström, S. R. Palumbi, J. M. Pandolfi, B. Rosen, and J. Roughgarden. 2003. Climate change, human impacts, and the resilience of coral reefs. *Science,* 301:929–933.

Hughes, T. P., N. A. J. Graham, J. B. C. Jackson, P. J. Mumby, and R. S. Steneck. 2010. Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology and Evolution,* 25:633–642.

Jokiel, P. L. 1978. Effects of water motion on reef corals. Journal of Experimental Marine *Biology and Ecology,* 35:87–97.

Knudby, A., S. Jupiter, C. Roelfsema, M. Lyons, and S. Phinn. 2013. Mapping coral reef resilience indicators using field and remotely sensed data. *Remote Sensing,* 5:1311–1334.

Kohler, K. E., and S. M. Gill. 2006. Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Computers and Geosciences,* 32:1259–1269.

Lange, I. D., Perry, C. T., & Alvarez-filip, L. 2020. Carbonate budgets as indicators of functional reef “ health ”: A critical review of data underpinning census-based methods and current knowledge gaps. *Ecological Indicators*, 110 (October 2019)

Maynard, J. A., P. A. Marshall, J. E. Johnson, and S. Harman. 2010. Building resilience into practical conservation: Identifying local management responses to global climate change in the southern Great Barrier Reef. *Coral Reefs,* 29:381–391.

Maynard, J. A., S. McKagan, L. Raymundo, S. Johnson, G. N. Ahmadia, L. Johnston, P. Houk, G. J. Williams, M. Kendall, S. F. Heron, R. van Hooidonk, E. Mcleod, D. Tracey, and S. Planes. 2015. Assessing relative resilience potential of coral reefs to inform management. *Biological Conservation,* 192:109–119.

Maynard, J., S. McKagan, S. Johnson, and P. Houk. 2012. Coral reef resilience to climate change in Saipan , CNMI ; field-based assessments and implications for vulnerability and future management.

McClanahan, T. R., N. A. J. Graham, M. A. MacNeil, N. A. Muthiga, J. E. Cinner, J. H. Bruggemann, and S. K. Wilson. 2011. Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. *Proceedings of the National Academy of Sciences,* 108:17230–17233.

McClanahan, T. R., S. D. Donner, J. A. Maynard, M. A. MacNeil, N. A. J. Graham, J. Maina, A. C. Baker, J. B. Alemu I., M. Beger, S. J. Campbell, E. S. Darling, C. M. Eakin, S. F. Heron, S. D. Jupiter, C. J. Lundquist, E. McLeod, P. J. Mumby, M. J. Paddack, E. R. Selig, and R. van Woesik. 2012. Prioritizing Key Resilience Indicators to Support Coral Reef Management in a Changing Climate. *PLoS ONE*, 7.

McLean, M., J. Cuetos-Bueno, O. Nedlic, M. Luckymiss, and P. Houk. 2016. Local stressors, resilience, and shifting baselines on coral reefs. *PLoS ONE,* 11:1–17.

Moberg, F., and C. Folke. 1999. Ecological goods and services of coral reef ecosystems. *Ecological Economics*, 29:215–233.

Mumby, P. J., S. Bejarano, Y. Golbuu, R. S. Steneck, S. N. Arnold, R. van Woesik, and A. M. Friedlander. 2012. Empirical relationships among resilience indicators on Micronesian reefs. *Coral Reefs,* 32:213–226.

Mumby, P. J., N. H. Wolff, Y. Bozec, I. Chollett, P. Halloran, and M. Bode. 2014. Operationalizing the Resilience of Coral Reefs in an Era of Climate Change. *Conservation Letters,* 7:176–187.

Munk, W. H., and M. C. Sargent. 1948. Adjustment of Bikini Atoll to Ocean Waves. *American Geophysical Union,* 29.

Nyström, M., N. A. J. Graham, J. Lokrantz, and A. V. Norström. 2008. Capturing the cornerstones of coral reef resilience: Linking theory to practice. *Coral Reefs,* 27:795–809.

Nyström, M. 2009. Redundancy and Response Diversity of Functional Groups: Implications for the Resilience of Coral Reefs. *AMBIO: A Journal of the Human Environment*, 35:30–35.

Nyström, M. 2006. Redundancy and Response Diversity of Functional Groups: Implications for the Resilience of Coral Reefs. *AMBIO: A Journal of the Human Environment*, 35:30–35.

Nyström, M., C. Folke, and F. Moberg. 2000. Coral reef disturbance and resilience in a human-dominated environment. *Trends in Ecology and Evolution*, 15:413–417.

Obura, D., and G. Grimsditch. 2009. Resilience Assessment of Coral Reefs bleaching and thermal stress. *IUCN Climate Change and Coral Reefs Marine Working Paper Series*, 5

Perry, C. T., Edinger, E. N., Kench, P. S., Murphy, G. N., Smithers, S. G., Steneck, R. S., & Mumby, P. J. (2012). Estimating rates of biologically driven coral reef framework production and erosion : a new census-based carbonate budget methodology and applications to the reefs of Bonaire. *Coral Reefs*, 31:853–868.

Pfisterer, A. B., & Schmid, B. (2002). Diversity-Dependent Production Can Decrease the Stability of Ecosystem Diversity-dependent production can decrease the stability of ecosystem functioning. *Nature*, 416: 84–86.

Pratchett, M. S., M. Trapon, and M. L. Berumen. 2011. Recent disturbances augment community shifts in coral assemblages in Moorea , French Polynesia. *Coral Reefs*, 30:183–193.

Reynods, T. (2016). Environmental factors explain coral demography and coral bleaching patterns in Guam. *University of Guam*.

Riegl, B., P. W. Glynn, E. Wieters, S. Purkis, C. D'Angelo, and J. Wiedenmann. 2015. Water column productivity and temperature predict coral reef regeneration across the Indo-Pacific. *Scientific Reports,* 5:1–7.

Rohweder, J., J. T. Rogala, B. L. Johnson, and D. Anderson. 2012. Application of Wind Fetch and Wave Models for Habitat Rehabilitation and Enhancement Projects -2012 Update.

Rosenzweig, M. L. (1971). Paradox of Enrichment : Destabilization of Exploitation Ecosystems in Ecological Time. *American Association for the Advanced of Science*, 171(3969), 385–387.

Rowlands, G., S. Purkis, B. Riegl, L. Metsamaa, A. Bruckner, and P. Renaud. 2012. Satellite imaging coral reef resilience at regional scale. A case-study from Saudi Arabia. *Marine Pollution Bulletin*, 64:1222–1237.

Salm, R. V., S. E. Smith, and G. Llewellyn. 2001. Mitigating the impact of coral bleaching through marine protected area design. *Coral Bleaching: Causes, Consequences and Response*

Salm, R., and T. N. Conservancy. 2016. Chuuk Reef Health and Resilience Assessment Citizen Science Team Observations Chuuk Reef Health and Resilience Assessment Citizen Science Team Observations (17 July to 03 August 2016)

Schmitt, R. J., Holbrook, S. J., Davis, S. L., Brooks, A. J., & Adam, T. C. (2019). Experimental support for alternative attractors on coral reefs. *Proceedings of the National Academy of Sciences of the United States of America*, 116(10), 4372–4381.

Van Woesik, R., K. Sakai, A. Ganase, and Y. Loya. 2011. Revisiting the winners and the losers a decade after coral bleaching. *Marine Ecology Progress Series*, 434:67–76.

Van Woesik, R., P. Houk, A. L. Isechal, J. W. Idechong, S. Victor, and Y. Golbuu. 2012. Climate-change refugia in the sheltered bays of Palau: Analogs of future reefs. *Ecology and Evolution*, 2:2474–2484.

Webster, N. S., S. Uthicke, E. S. Botté, F. Flores, and A. P. Negri. 2013. Ocean acidification reduces induction of coral settlement by crustose coralline algae. *Global Change Biology,* 19:303–315.

West, J. M., and R. V. Salm. 2003. Resistance and resilience to coral bleaching: implications for coral reef conservation and management. *Wiley Online Library*, 17:956–967.

Appendix

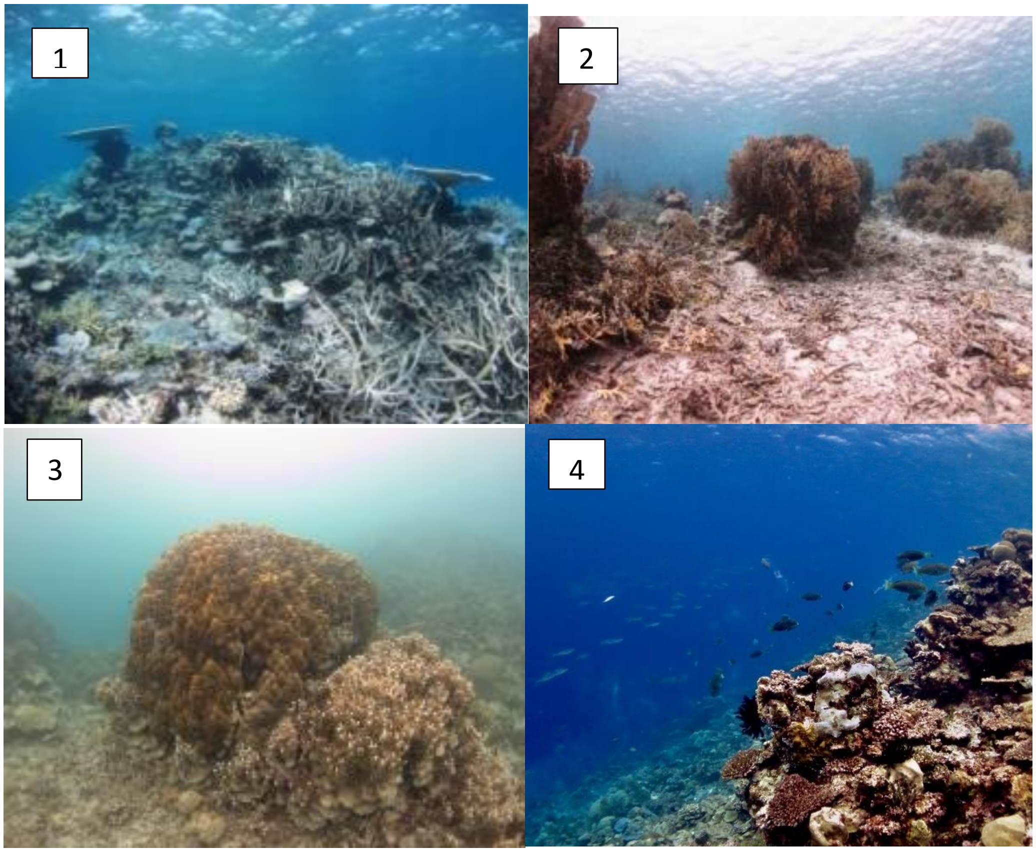


Figure 19: Representational photos of Chuuk reef types; (1) patch/back reef (2) channel reef (3) inner reef (4) outer reef

Table 7: Study sites of 2016 rapid assessment compared with 2021 predicted vs. observed study sites for channel and inner reef types

2016 rapid assessment site names	2021 Predicted vs. Observed Resilience Study	Reef type
C-14	CHK-10	channel
C-10	CHK-12	channel
C-35	CHK-13	channel
C-77	CHK-135	channel
C-11	CHK-20	channel
C-37	CHK-3	channel
C-33	CHK-451	channel
C-46	CHK-56	channel
C-50	CHK-77	channel
C-309		channel
C-301		channel
C-303		channel
C-203		channel
C-206		channel
Parem	CHK-116	inner
Uman	CHK-16	inner
C-311	CHK-18	inner
C-58	CHK-19	inner
C-312	CHK-2	inner
Onei MPA	CHK-40	inner
C-307	CHK-514	inner
C-3	CHK-98	inner
C-17		inner
C-75		inner
Pisinini Inner		inner
Kuop *Acropora* Garden		inner
Onei Ref		inner

Table 8: Study sites of 2016 rapid assessment compared with 2021 predicted vs. observed study sites for outer and patch/back reef types

2016 rapid assessment site names	2021 Predicted vs. Observed Resilience Study	Reef type
C-61	CHK-2237	outer
C-208	CHK-24	outer
C-209	CHK-25	outer
C-212	CHK-27	outer
C-213	CHK-28	outer
C-48	CHK-33	outer
C-49	CHK-34	outer
C-12	CHK-43	outer
C-45	CHK-855	outer
C-13		outer
C-201		outer
C-40		outer
C-41		outer
C-300		outer
C-34		outer
C-57		outer
C-305		outer
C-55		outer
C-202		outer
C-204		outer
C-205		outer
C-207		outer
C-52		outer
C-6	CHK-1	patch/back
C-39	CHK-11	patch/back
C-210	CHK-15	patch/back
Onei-3	CHK-1542	patch/back
C-1	CHK-17	patch/back
C-42	CHK-31	patch/back
C-308	CHK-348	patch/back
C-59	CHK-36	patch/back
C-36	CHK-4	patch/back
C-16	CHK-44	patch/back
C-310	CHK-50	patch/back
C-62	CHK-59	patch/back
C-15		patch/back
C-211		patch/back
C-44		patch/back
C-5		patch/back
C-7		patch/back
C-9		patch/back
C-18		patch/back
C-38		patch/back
C-4		patch/back
C-60		patch/back
C-8		patch/back
C-47		patch/back
C-53		patch/back
C-302		patch/back
C-306		patch/back
C-302 ext		patch/back

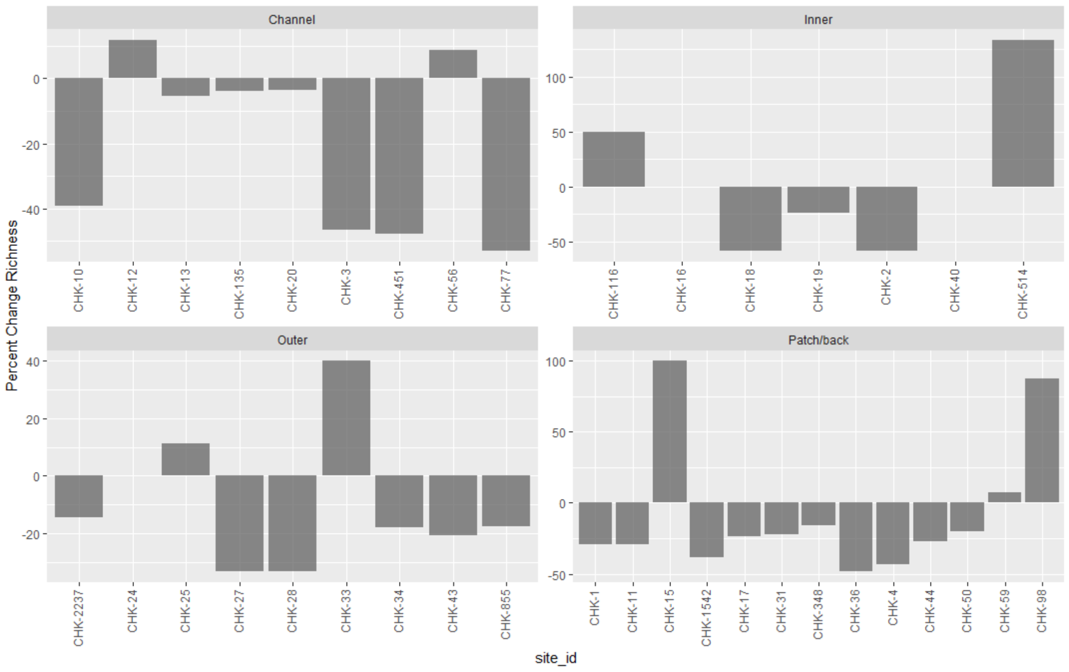


Figure 20: Percent change in richness from earliest recorded to most recent measurement across all study sites, grouped by reef type.

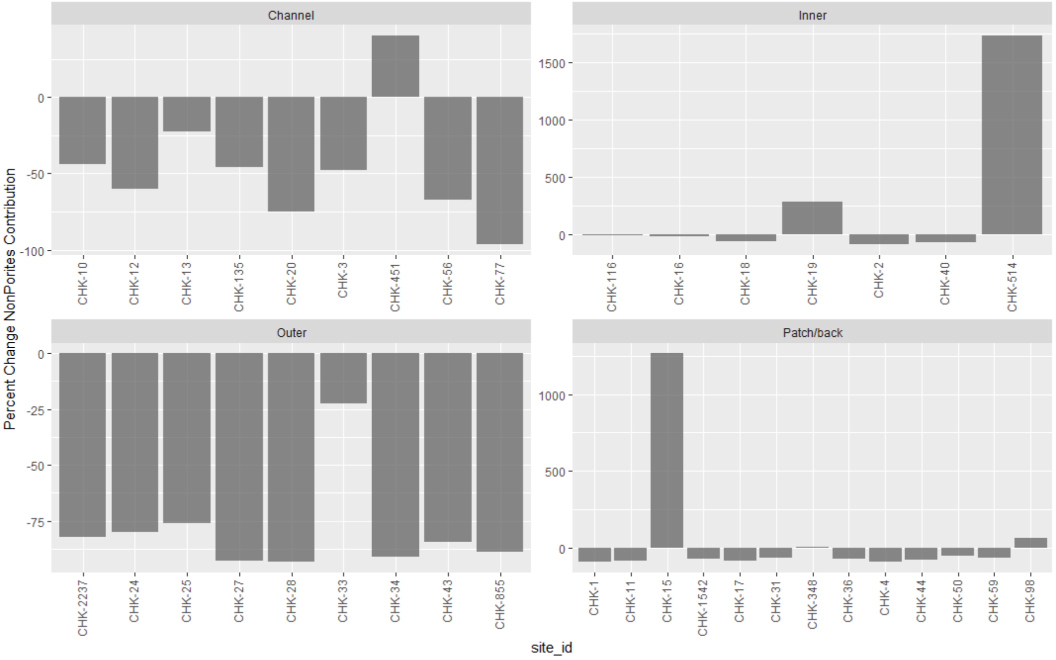


Figure 21: Percent change in non-*Porites* contribution from earliest recorded to most recent measurement across all study sites, grouped by reef type.

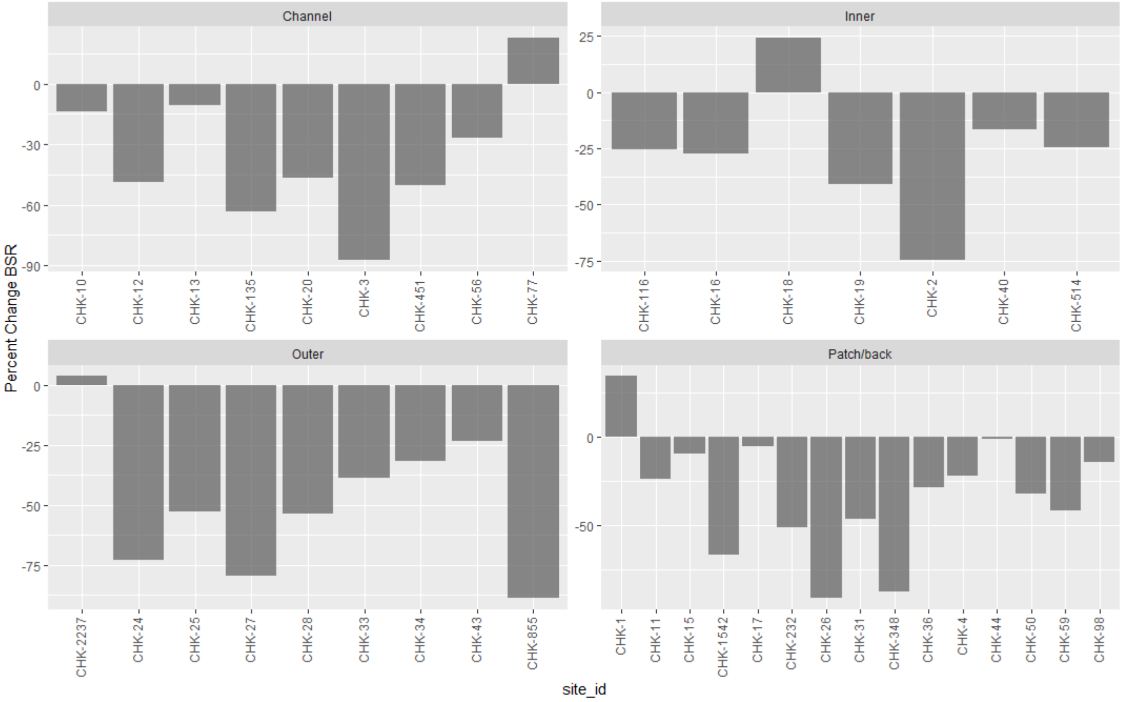


Figure 22: Percent change in benthic substrate ratio from earliest recorded to most recent measurement across all study sites, grouped by reef type.