Evaluating Coral Reef Recovery Four Years Post-bleaching and Assessing the Effectiveness of Pre-bleaching Reef Resilience Rankings

Photo by TNC 2017

This report was prepared by The Nature Conservancy with financial the National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Office of Habitat Conservation as administered by the Office of Habitat Conservation through award NA17NMF4630301. These data and related items of information have not been formally disseminated by NOAA, and do not represent any agency determination, view, or policy.

Evaluating Coral Reef Recovery Four Years Post-bleaching and Assessing the Effectiveness of Pre-bleaching Reef Resilience Rankings

by

Dwayne Minton[1], Eric Conklin[2], Ryan Carr[2], Hank Lynch[2], Julia Rose[2], Zach Caldwell, and Rebecca Most[2]

[1]Dwayne Minton Consultants
B-2434 Perrier Ln.
Nelson, BC V1L7C3
Canada

[2]The Nature Conservancy
923 Nu'uanu Ave.
Honolulu, HI 96817

June 17, 2020

Table of Contents

Cover Photo: A mixed school of surgeonfish graze across a West Hawai‘i reef.

1.0 Executive Summary

Coral reef resilience is the capacity of a reef to resist and/or recover from degradation and maintain provisions of ecosystem functions and services. Resilience-based management often entails applying information about the spatial variation in resilience potential to aid managers with targeting and tailoring actions to preserve or restore the resilience of reefs. Resilience potential can be assessed by measuring several resilience indicators across sites and producing aggregate scores that expresses resilience potential for each site relative to the site with the highest assessed resilience potential.

In the fall of 2015, The Nature Conservancy (TNC) with its partners assessed the relative resilience potential of twenty reef locations along the west coast of Hawaiʻi Island (West Hawaiʻi), focusing on the reefs in the NOAA Habitat Focus Area in the districts of South Kohala and North Kona. At each of these locations, both shallow (5-7 m) and deep (12-15 m) sites were surveyed, resulting in a total of 40 sites included in the resilience assessment. During these surveys, West Hawaiʻi was undergoing a mass coral bleaching event that affected nearly all coral species and extended to sites at least as deep as 15 m. Follow-up surveys in 2016 and 2017 documented considerable coral mortality and some early indications that the reefs had stabilized and may have been recovering. In 2019, TNC and its partners returned to the same reef locations and repeated the surveys, with the following objectives: 1) assess the condition of the previously-surveyed reef sites four years after the 2015 mass bleaching event, and 2) evaluate the resistance and recovery of these reef sites relative to the rankings determined in the 2015 reef resilience assessment.

Twenty-seven coral species were identified during the 2019 surveys with *Porites lobata* (lobe coral) and *P. compressa* (finger coral) accounting for over 91% of all coral observations. Coral cover has not changed significantly since the 2016 surveys, holding steady at 19.6 ± 1.6%, but continued to remain significantly lower than in 2015 (25.5 ± 1.6%) due to extensive bleaching-related mortality. During the 2019 survey effort, West Hawaiʻi reefs were undergoing another mass bleaching event. Although not as severe as the 2015 bleaching event, 22.8 ± 1.8% of coral colonies were experiencing some level of bleaching, and coral disease prevalence had increased from 2017, rising from 2.5 ± 0.4% to 3.8 ± 0.5% of colonies showing at least one disease. Five coral diseases (*Porites* Growth Anomalies, *Porites* Tissue Loss Syndrome, *Montipora* Growth Anomalies, *Pocillopora* Tissue Loss Syndrome and *Porites* Trematodiasis) and two other compromised health conditions (algal overgrowth and bleaching) were identified, with algal overgrowth being the most prevalent disease/condition affecting corals on West Hawaiʻi.

While coral cover appears to have stabilized across study sites, coral recruitment appears to have declined and has shown a downward trajectory since the original 2015 surveys. This trend raises concerns about the long-term ability of these reef locations to recover from the 2015 and future stress events. The underlying cause(s) of the declining recruitment is not clear, but it could be associated with numerous factors that affect larval supply and post-settlement recruit mortality.

A total of 117 species of reef fish in 26 families were observed in 2019. The families Acanthuridae (surgeonfishes) and Scaridae (parrotfishes) contributed the most to total fish biomass. Herbivores accounted for approximately half of all the total fish biomass, whereas apex

predators were rarely observed. Total fish biomass rebounded from a low in 2017 to 60.8 ± 12.7 g/m^2, which was not different from that observed in 2016 (71.1 ± 9.8 g/m^2) but significantly lower than that observed in 2015 (79.6 ± 4.6 g/m^2). While a decline associated with the 2015 mass coral bleaching event cannot be ruled out, these fluctuations in fish biomass are likely associated with natural spatial and temporal variability in reef fish populations.

To assess the ability of the 2015 resilience rankings to “predict” which sites would be resistant to or best able to recover from the 2015 bleaching event, three measures of reef resilience were estimated from the 2015-2019 survey data. These measures included two measures of a site's resistance and one measure of recovery, and were compared against the original resilience rankings. These 2015 rankings used unweighted indicator scores, meaning all resilience indicators were considered of equal importance when creating the rankings. The rankings were also recalculated using weightings obtained from the scientific literature. The unweighted and weighted rankings were not correlated with any of the measures of resistance and recovery, suggesting the rankings developed in 2015 were not effective at predicting a site's relative resilience to thermal stress. Application of indicator weightings had a small effect on the rankings, with no site shifting more than 3 positions and sites that originally had the highest and lowest scores changing little.

Attempts were made to further refine the rankings, but proved unsuccessful because of limitations associated with the available statistical methods and our nascent understanding of the complexities associated with reef resilience, including a clear expectation of the time frame over which recovery dynamics are expected to manifest (*i.e.*, is four years post-bleaching enough time?). While beyond the scope of this study, the path forward may benefit from a deconstructionist approach to the resilience concept. Separating the resistance and recovery components of resilience may also provide greater insight into to threats affecting Hawai‘i's reefs, and may improve management efforts in the long run.

2.0 Introduction

The west coast of Hawai‘i Island (hereafter West Hawai‘i) contains one of the longest contiguous coral reef systems in the main Hawaiian Islands, which are home to culturally and economically significant species, mitigate wave and storm impacts, and provide recreational and other economic benefits to the residents of the state (Cesar and van Beukering 2004). Reducing the degradation and improving the resilience of these marine ecosystems is a goal within many management plans for West Hawai‘i and is regularly mentioned as important by stakeholders.

Coral reef resilience is the capacity of a reef to resist and/or recover from degradation and maintain provisions of ecosystem functions and services (Mumby *et al.* 2007). Resilience encompasses two key components; resistance is the ability of a reef to resist or survive a disturbance, and recovery is the ability of a reef to return to its original condition following a disturbance (West and Salm 2003). Resilience is especially important within the context of climate change, under which global stressors including rising ocean water temperature and acidification are exerting increasing stress on coral reef ecosystems worldwide and contributing to reef degradation and loss.

Resilience-based management involves the application of resilience theory and tools to deliver ecosystem-based management outcomes into the future (Chapin *et al.* 2009, Maynard *et al.* 2015). Often for coral reefs, this involves assessing indicators/processes thought to make reefs more resistant to thermal events (*e.g.*, temperature resistance, etc.) and better able to recover from an adverse effect (*e.g.*, recruitment, etc.). This information is then used to target and tailor actions to preserve or restore the resilience of reefs (Weeks and Jupiter 2013, Maynard *et al.* 2015). Typically, these assessments involve measuring resilience indicators across several sites and producing aggregate scores that expresses "resilience potential" for each site relative to the site with the highest assessed resilience potential. Such assessments have been recommended by coral reef scientists, managers, and leading conservation organizations (McClanahan *et al.* 2012, Graham *et al.* 2013, Anthony *et al.* 2015, Maynard *et al.* 2017).

This type of guidance would be valuable in Hawai‘i because warm water conditions sufficient to trigger coral bleaching events are expected to occur annually in the state by the middle of the century (van Hooidonk *et al.* 2014). Given the slow natural recovery rates for most coral species, frequent and repeated bleaching events would likely decrease coral cover and alter species composition, degrading coral reefs and the cultural, recreational, tourism and coastal protection benefits they provide to island communities. Changes in the coral assemblage would also create cascade effects through the coral reef ecosystem that would likely reduce fish species abundance and alter fish assemblage composition (Garpe *et al.* 2006, Bellwood *et al.* 2016), causing a disruption to commercially and culturally important fisheries.

In October 2015, The Nature Conservancy (TNC) with partners at SymbioSeas, the Hawai‘i Division of Aquatic Resources (DAR), NOAA's Ecosystems Science Division[1] (ESD), the Hawai‘i Institute of Marine Biology (HIMB), and community organizations in West Hawai‘i

---

[1] This group was previously known as NOAA's Coral Reef Ecosystems Division/Program (CRED/CREP)

assessed the relative resilience[2] of 20 reef locations within priority areas of the South Kohala and North Kona Districts along the west coast of Hawaiʻi Island. At the time these surveys were conducted, a prolonged period of elevated sea water temperatures had resulted in the onset of widespread coral bleaching on West Hawaiʻi reefs (Kramer *et al.* 2016, Maynard *et al.* 2016). During this period, sea temperatures had been above the bleaching threshold (Degree Heating Weeks = 4 °C-weeks) for two months (NOAA CRW 2016), a level of thermal stress unprecedented in Hawaiʻi. TNC's research team documented severe, widespread bleaching in nearly all coral species and down to depths of at least 15 m (Maynard *et al.* 2016). Due to its severity and duration, the bleaching caused significant coral mortality (Kramer *et al.* 2016, Minton *et al.* 2018a), the long-term consequences of which remain unclear but are the subject of ongoing research. In 2016 and 2017 TNC and its partners returned to the same reef locations and repeated the reef resilience and bleaching surveys and documented significant coral mortality, but also noted hopeful signs that recovery may be underway (Minton *et al.* 2018a, Minton *et al.* 2018b).

TNC returned to these locations in 2019, four years after the mass coral bleaching event, to again document the condition and recovery of West Hawaiʻi reefs to this unprecedented mass bleaching event. In addition, these new data were intended to allow for deeper exploration of the effectiveness of the resilience rankings developed in 2015 in predicting the ability of Hawaiʻi reefs to respond to a changing climate. This report describes the results of the 2019 surveys and builds upon pre-existing information to assess the current condition and trajectory of these 20 West Hawaiʻi reef locations.

---

[2] While the specific approach used focused on resilience to thermal stress, it was expected that the indicators selected also would apply more generally to resilience processes.

3.0 Methods

The survey methods have been described in detail previously (Maynard *et al.* 2016, Minton *et al.* 2018a), and are summarized here. The purpose of these methods was originally to collect data in 2015 on specific indicators of reef resilience that could be used to create a relative ranking of the sites that would be reflective of their resilience to the effects of climate change. The same methods have continued to be used in subsequent surveys to assess the response of the marine resources at each site to the 2015 mass coral bleaching event.

Numerous reef resilience indicators proposed in the scientific literature were examined by McClanahan *et al.* (2012) and ranked based on their perceived importance, scientific evidence supporting their linkage to resilience, and their feasibility of measurement. Eleven indicators were selected from this assessment by a suite of Hawaiʻi coral reef scientists and managers for investigation at West Hawaiʻi (Maynard *et al.* 2016). Seven biological indicators, including six identified by McClanahan *et al.* (2012) (coral cover, coral diversity, coral recruitment, bleaching resistance, macroalgae cover, and herbivorous fish biomass) and rugosity[3], were used to create an aggregate resilience score and ranking. The remaining five indicators (temperature variability, nutrients, sedimentation, physical human impacts, and fishing pressure) were used to investigate linkages between these environmental indicators and site resilience, the results of which have been discussed in greater detail elsewhere (Minton *et al.* 2018a).

3.1 Locations and Sites

The NOAA ESD, NOAA Habitat Blueprint, and Sentinel Site Program have an overlapping Focus Area in West Hawaiʻi. These programs have consolidated their efforts to gather information and provide support for effective management of marine resources in this area. The Focus Area also overlaps with, and is supported by, the NOAA Hawaiian Islands Humpback Whale National Marine Sanctuary, and is a focus of the NOAA National Marine Fisheries West Hawaiʻi Integrated Ecosystems Assessment Project.

In 2015, reef resilience was assessed at twenty locations selected in consultation with DAR, extending from the North Kona to South Kohala Districts of West Hawaiʻi (Figure 1). Eighteen locations were spaced approximately ~2.5 kilometers apart within the Focus Area using ArcGIS and should be representative of the full range of the area's ecological and physical conditions. At the request of the DAR, two additional locations south of the Focus Area (Honokōhau and Keauhou) were also surveyed (Figure 1). At DAR's request, seven of the selected locations overlapped with existing DAR West Hawaiʻi monitoring sites. At each location, a shallow (5-7 m) and deep (12-15 m) site were surveyed, resulting in a total of 40 sites included in the assessment. Location metadata are provided in Appendix A.

The mass bleaching event that occurred in 2015 presented a unique opportunity to examine the response of West Hawaiʻi's reefs to temperature stress, as well as to evaluate the short-term predictive potential of the 2015 reef resilience rankings. For this reason, TNC decided to return

---

[3] Benthic rugosity is often correlated with abundance and diversity of associated species, especially fish (Friedlander and Parrish 1998).

to these sites to repeat the reef resilience methodology in 2016. Site photos, field notes, GPS coordinates, and compass bearings collected in 2015 were used to realign transects for re-surveying in 2016, and stainless steel pins were installed at the start and end of each transect to permanently mark them for future resurveys which occurred again in 2017 (see Minton *et al.* 2018b) and 2019 (this report). At the request of DAR, transects at locations that overlapped with existing DAR monitoring sites were offset at least 100 m from the original 2015 location to avoid interference with their ongoing monitoring efforts. Because we could not resurvey the exact same sections of reef from 2015 to 2016, additional spatial variability was likely introduced into comparisons made with the 2015 data that was not present among comparisons for other survey years. While Minton *et al.* (2018a) showed the effects of the bleaching event were much larger than the variability introduced from the spatial shift in transect position, and that the shifting of transects introduced no systematic bias into those findings, for some analyses in this report, we have decided to removed sites with an offset between the 2015 and 2016 transect start location >35 m when conducting multi-year analyses that include 2015 survey data (see section 3.3.2 for more discussion).

3.2 Field Assessments

At all locations, we conducted comprehensive assessments to document spatial patterns of species abundance, biomass and condition. Survey work was completed between October 22 and November 6, 2019, which corresponded

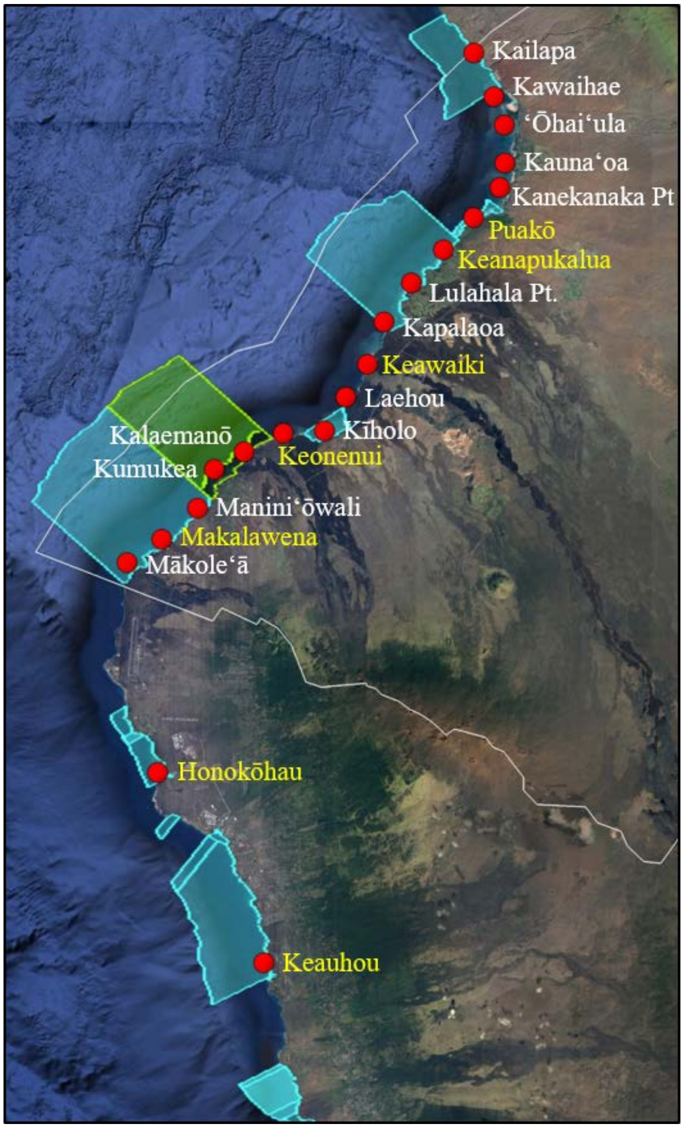

Figure 1. Map of survey locations, at each of which a shallow and deep site were surveyed. The white line is the boundary of the NOAA's West Hawaiʻi Focus Area. Blue polygons are State of Hawaiʻi Fishery Management Areas (FMAs) and Fishery Replenishment Areas (FRA). Both FMAs and FRAs have additional fishing restrictions compared to "open" areas. The green polygon is the Ka'ūpūlehu Marine Reserve. Two survey location (Kumukea and Kalaemanō) are within the nearshore section of the Marine Reserve, which was closed to all fishing on July 29, 2016. Prior to closure, the Ka'ūpūlehu Marine Reserve was an FRA. Locations highlighted in yellow overlap with DAR Monitoring sites. See text for additional discussion.

with the timeframe during which surveys in previous years were conducted (late September and early November). Surveys were conducted along three replicate 25-m transect lines laid out consecutively within the defined depth ranges at both shallow and deep sites within each location. An intervening space of ~10 m was left between the end of one transect and the start of the next. Depending on the type of data collected, all or part of each transect line was surveyed (see Table 1 for more information). Assessments were conducted by a three- or four-person team, comprised of surveyors who were trained and calibrated to reduce observer variability and produce credible data. The method for each survey type is summarized in Table 1, with more-detailed descriptions in Appendix B.

3.3 Analysis

All fish and site data were entered into a custom Access database and checked for errors. All benthic data were compiled and verified in either Excel spreadsheets (benthic cover) or using the R statistical package (coral health) prior to analysis. All databases and spreadsheets support safeguards to ensure high data quality, and they reside on a secure, central TNC server that is backed up daily to an offsite location to protect against data loss.

3.3.1 Reef Condition and Coral Health

The benthic assemblage was characterized by percent cover by benthic type/group (*e.g.*, all coral, all macroalgae, abiotic, etc.), and where there existed sufficient taxonomic resolution (*e.g.*, coral), to species. Overall coral health was examined using disease (DZ) and compromised health (COMP) condition prevalence, calculated as follows:

$$\text{Prev} = \frac{\text{\# of colonies with at least 1 type of DZ or COMP}}{\text{\# of total colonies}}$$

The prevalence of each genera-specific disease was calculated as follows:

$$\text{Prev}_{(\text{DZ or COMP})} = \frac{\text{\# of colonies with a specific DZ or COMP}}{\text{\# of total colonies or \# of colonies of a given genus}}$$

Species-specific fish biomass data were pooled into two groups: all fish and by trophic class. A 5-level trophic designation was used, including: herbivores (primary), piscivores (secondary), other carnivores (secondary), planktivores (secondary), and apex predators (tertiary). Trophic designations for each species were obtained primarily from FishBase (Froese and Pauly 2011), or from species-specific literature if Hawaiian populations were known to vary from the larger species.

3.3.2 Reduced Data Set

Initially, surveys were to be conducted only in 2015, so permanent transect markers were not installed. When an opportunity to repeat the surveys arose in 2016 and 2017, the decision was made to install permanent transect markers to reduce spatial variability in the data. At the request

Table 1. Summary of field survey methods used along each 25-m transect line (three replicate transects/site). See Appendix B for a more-detailed description of each method. Some data collection methods used only a portion of the 25 m transect, as described under the "Transect Area column.

Data Type	**Transect Area**	**Method**
Coral Health	0-10 m (1 m-wide belt)	All coral colonies were counted and identified to species. Each colony was inspected for signs of known diseases and other conditions (e.g., bleaching, algal overgrowth, etc.). The prevalence of each condition was calculated separately for each site and by species, as appropriate.
Coral Juveniles	0-10 m (1 m-wide belt)	All coral colonies ≤5 cm in diameter (longest dimension) whose geometric center lay within a 0.5 x 0.5 m quadrat were counted and identified to the lowest taxonomic level. Four quadrats were haphazardly spaced ~2 m apart within the coral health belt transect.
Rugosity	0-10 m	A rugosity index was calculated by dividing the length of brass chain required to contour the bottom by the 10 m transect length. For this index, a value of one represents a flat surface with no relief, and increasing values represent more topographically complex substratum.
Benthic Cover	0-25 m	Photographs of the bottom were taken at every meter using a monopod, generating 25 images/transect. Twenty randomly-selected photographs from each transect were analyzed to estimate benthic cover. Due to lower taxonomic resolution in the 2015 survey data, when inter-annual comparisons were made, data were aggregated into four major benthic categories: corals, macroalgae, coralline algae, and other substrata.
Fish abundance and Size	0-25 m (5 m-wide belt)	All fish within or passing through a 5-m wide belt were identified to species and sized into 5-cm bins (*i.e.*, 0-5 cm, >5-10 cm, >10-15 cm, etc.). The weight of each fish in grams was calculated using standard weight-length relationships and using coefficients sourced from FishBase, the USGS Hawai‘i Cooperative Fishery Research Unit and NOAA's Coral Reef Ecosystem Program. Only herbivorous fish biomass was used in the resilience assessment.

of the DAR, TNC relocated the start position of any 2015 transect that corresponded with a DAR long-term monitoring site. This resulted in a >100 m offset of the 2015 and 2016 transects at these locations (Table 2), and likely placed the 2016 transects in substantially different reef areas from those surveyed in 2015. As such, these sites may no longer be as representative of change since the 2015 bleaching event as sites with smaller offsets, so any site with an offset >35 m was removed from any multi-year analysis that included the year 2015. This "reduced" dataset included a total of 27 sites, of which all but three transects had offsets <25 m, which was below the spatial resolution of the original 2015 survey data. For analyses that used only a single year, the "full" dataset was used. To distinguish between the datasets throughout this report, the "full" data comprised all survey sites and the "reduced" data comprised only sites with an offset <35 m.

3.3.3 Statistical Analyses

All means are presented as the average ± the standard error of the mean (SEM) unless otherwise stated. Data for each site was obtained by averaging across the three transects. Standard parametric and non-parametric statistical approaches, as appropriate, were used to test for differences between depth and among years. Time series analyses using the reduced 2015-2019 dataset were conducted using a mixed model ANOVA with time and depth as fixed factors and

---

Table 2. Offset (m) in the transect start locations between the 2015 survey sites and the permanent transects installed in 2016. Offset is for the first transect at each site. Only sites with an offset <35 m ("x" in the reduced dataset column) were included from the reduced dataset used in some analyses (see section 3.3.2).

Shallow Sites	Offset (m)	Reduced Dataset	Deep Sites	Offset (m)	Reduced Dataset
Kailapa	23.3	x	Kailapa	26.9	x
Kawaihae	10.1	x	Kawaihae	18.8	x
ʻŌhaiʻula	5.6	x	ʻŌhaiʻula	10.5	x
Kauna'oa	2.6	x	Kauna'oa	6.9	x
Kanekanaka Pt.	14.0	x	Kanekanaka Pt.	29.0	x
Puakō	203.4		Puakō	203.0	
Keanapukalua	34.3	x	Keanapukalua	102.5	
Lulahala Pt.	28.3	x	Lulahala Pt.	3.5	x
Kapalaoa	13.7	x	Kapalaoa	7.2	x
Keawaiki	61.7		Keawaiki	109.4	
Laehou	9.3	x	Laehou	9.4	x
Kīholo	20.7	x	Kīholo	14.9	x
Kalaemanō	3.5	x	Kalaemanō	3.4	x
Keonenui	12.0	x	Keonenui	78.7	
Kumukea	9.0	x	Kumukea	12.2	x
Manini'ōwali	17.1	x	Manini'ōwali	11.1	x
Makalawena	135.8		Makalawena	159.5	
Mākoleʻā	12.1	x	Mākoleʻā	2.6	x
Honokōhau	158.7		Honokōhau	124.5	
Keauhou	241.3		Keauhou	247.5	

site as a random factor to account for the non-independence of repeated measures at survey sites. Models were run for percent coral cover, coral colony density, coral recruit density, and biomass of all fish. Fish biomass was log+1 transformed to correct skewness and improve heteroscedasticity prior to analysis. Given the natural variability of coral reef ecosystems, we considered statistical significance to be $p_{adj} \leq 0.05$ and "marginal" significance to be $0.05 < p_{adj} \leq 0.10$. Model fits were assessed by examining the distribution of model residuals, Cook's distances with values greater than 4/n as the threshold for influential data points, and leverage. A-posteriori comparisons among the years were conducted on unweighted least-squares means using a Tukey adjustment to control the overall error rate. The time series analyses were conducted using the 'lme4' and 'lsmeans' packages in R version 3.6.1 (2019-07-05).

3.3.4 Resilience Rankings

Resilience rankings were initially calculated using data collected in 2015 (Maynard *et al.* 2016), with separate resilience rankings calculated for each depth stratum. Each indicator was normalized to a unidirectional scale of 0-1 by dividing by the maximum value for the variable among all 20 sites within the depth strata. To ensure that high indicator values always inferred higher relative resilience potential, normalized values were inverted for macroalgae, and all indicators were equally weighted. Resilience scores were calculated by averaging the normalized indicator values for each site, after which these aggregated scores were also normalized. Sites were then ordered by score and ranked from 1 (highest rank) to 20 (lowest rank). These rankings were intended to express the resilience of all sites relative to the site with the highest score, *i.e.*, the final normalized scores ranged from 0-1 and represented decimal percentages of the site with the highest score (1.00).

At the time, it was unclear if weighting indicators was beneficial, so the decision was made not to weight the indicators when calculating the resilience score. To examine the efficacy of this decision, in this report we have recalculated the 2015 resilience rankings and weighted them based on differences in the perceived importance (R_{WP}) and scientific evidence supporting their linkage to resilience (R_{WS}) of each from Table 2 in McClanahan *et al.* (2012). Of our seven indicators, bleaching resistance had the highest scores for both perceived importance and scientific evidence, 15.57 and 7.15 respectively, and rugosity had the lowest scores, 9.19 and 2.26, respectively. Following the approach used by Maynard *et al.* (2015), we derived the weightings by dividing the perceived importance and scientific evidence scores for each indicator by the lowest indicator score to produce two sets of weighting multipliers (Table 3).

When the weightings were applied, the effect on the rank for a given site was minor compared to the unweighted rankings, especially for the shallow sites (Table 4; Figure 2). Among shallow sites only the top two ranked sites switched positions for the R_{WP} and no site moved >2 positions for the R_{WS} relative to the unweighted 2015 rankings. Rankings were not as consistent for deep sites, but still no ranking changed position by >3 positions for either the R_{WP} or R_{WS}. In general, the positions of sites at the high and low ends of the rankings changed little regardless of the weighting approach employed.

Table 3. Weighting multipliers for each resilience indicator derived from the perceived importance and the scientific evidence supporting their linkage to resilience as reported in Table 2 of McClanahan *et al.* (2012). See text for information on how the weighting multipliers (W_P and W_S) were derived.

Variable	**Perceived Importance**	**W_P**	**Scientific Evidence**	**W_S**
Bleaching Resistance	15.57	1.69	7.15	3.16
Coral Diversity	12.43	1.35	4.11	1.82
Herbivorous fish biomass	11.75	1.28	4.96	2.19
Macroalgae	11.46	1.25	4.70	2.08
Coral recruitment	11.43	1.24	4.89	2.16
Coral Cover	9.50	1.03	3.14	1.39
Rugosity	9.19	1.00	2.26	1.00

Table 4. Rankings for shallow and deep sites using both the unweighted (R) and weighted (R_{WP} and R_{WS}) resilience indicators. Red numbers highlight difference between the unweighted and weighted rankings

Shallow	**R**	**R_{WP}**	**R_{WS}**	**Deep**	**R**	**R_{WP}**	**R_{WS}**
Laehou	1	2	2	Laehou	1	1	1
Kumukea	2	1	1	Kīholo	2	2	2
Kīholo	3	3	3	Puakō	3	4	6
Mākole'ā	4	4	5	Kumukea	4	3	3
Manini'ōwali	5	5	4	Makalawena	5	5	4
Keawaiki	6	6	8	Kauna'oa	6	6	5
Makalawena	7	7	7	'Ohae'ula	7	7	8
Keonenui	8	8	6	Honokōhau	8	10	10
Keanapukalua	9	9	11	Kailapa	9	9	11
Lulahala Pt.	10	10	9	Makole'a	10	8	7
Kalaemanō	11	11	12	Manini'owali	11	11	9
Kauna'oa	12	12	10	Keauhou	12	13	14
Keauhou	13	13	13	Keanapukalua	13	15	15
Kailapa	14	14	14	Keawaiki	14	12	13
Kawaihae	15	15	17	Kalaemanō	15	14	12
Kapalaoa	16	16	16	Kanekanaka Pt.	16	17	17
Honokōhau	17	17	15	Keonenui	17	16	15
'Ōhae 'ula	18	18	18	Kawaihae	18	18	18
Kanekanaka Pt	19	19	19	Kapalaoa	19	19	19
Puakō	20	20	20	Lulahala Pt	20	20	20

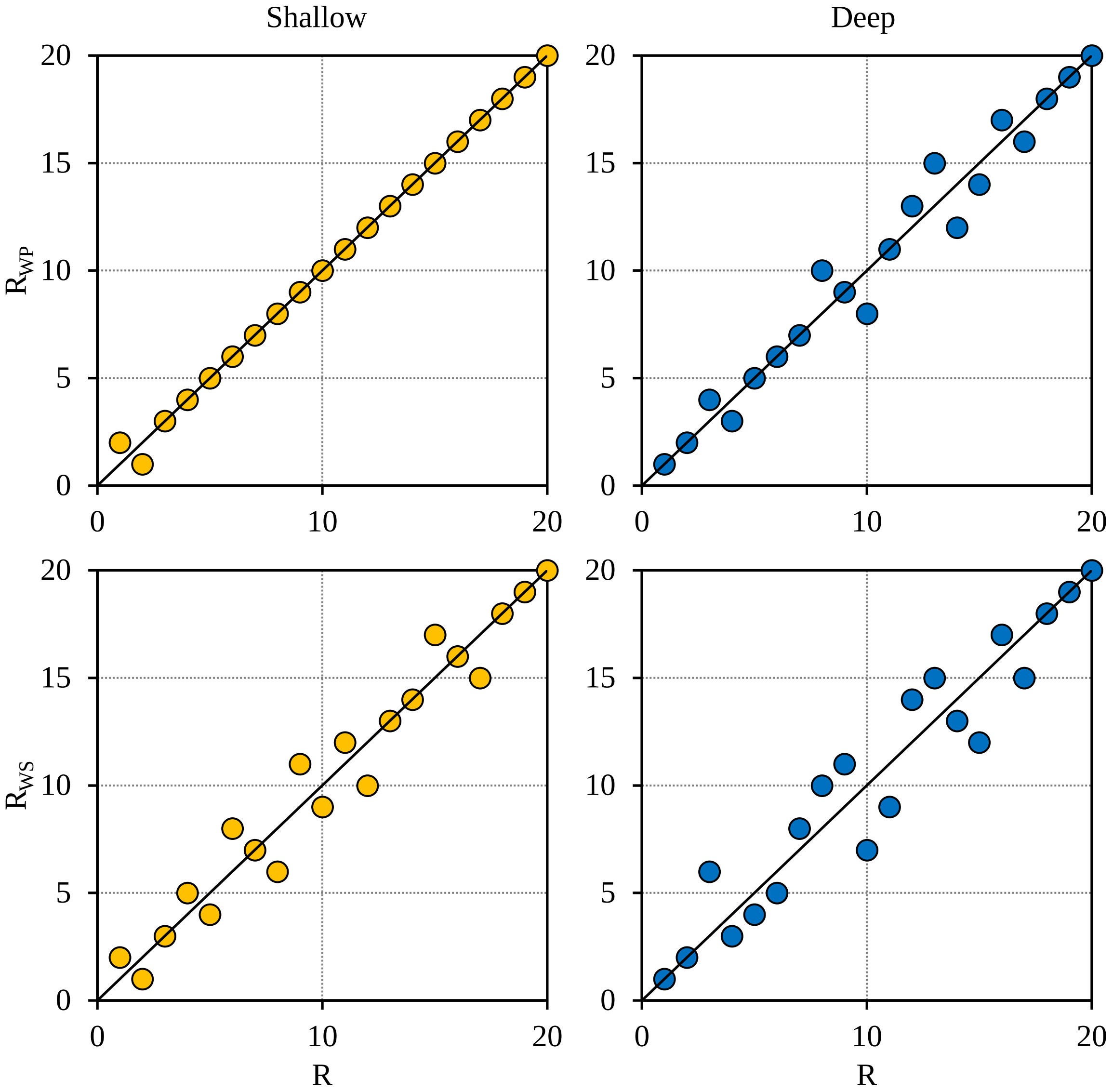

Figure 2. Relationship of unweighted (R) and weighted (R_{WP} and R_{WS}) relative resilience ranks for shallow (gold) and deep (blue) sites. The diagonal line represents congruence between the unweighted and weighted ranks, and if the point lies on the line, the ranks determined for the site using the unweighted and weighted approaches were identical.

To assess the effectiveness of the resilience rankings to "predict" site resilience, we compared unweighted and weighted rankings to measures of reef resistance and recovery derived from the reduced 2015-2019 dataset. Measures of resistance and recovery were generated from two "types" of data: cover-specific and colony-specific. Cover- and colony-specific data are not always correlated (Minton *et al.* 2018a), and it is possible that the rankings may perform well with one or both types of data. Resistance was estimated using two measures: 1) change in coral abundance from 2015 to 2016 (measured as the relative[4] change in percent cover and in coral density), and 2) amount of bleaching in 2019[5] (measured as percent of tissue bleached and bleaching prevalence). Bleaching rates from the 2015 event were not used as a measure of resistance because these values were used in the calculation of the reef resilience rankings. Recovery was estimated using one measure: relative change in coral abundance from 2016 to 2019 (measured as the relative change in percent cover and in coral density). Weighted (R_{WP} and R_{WS}) and unweighted (R) resilience rankings were correlated with resistance and recovery estimates using a Pearson's Product Moment.

---

[4] Confusion often results when discussing a decline in percent cover. *Absolute change* would be the change in percent cover from one year to the next, *i.e.*, $\%cover_{(2016)}$ - $\%cover_{(2015)}$, whereas *relative change* would be scaled relative to the initial year of the survey, *i.e.*, $(\%cover_{(2015)} - \%cover_{(2016)}) / \%cover_{(2015)}$. Relative change allows changes in cover at sites with different coverage of coral to be more easily compared.

[5] This assumes the thermal stress was roughly equivalent across all sites during the 2019 bleaching event. While fine spatial resolution data on thermal stress are lacking, information from NOAA's Coral Reef Watch (CRW), suggests some uniformity in the thermal stress across the survey area. CRW compiles and models bleaching-related oceanographic data at a 5 km spatial scale, however, which cannot account for localized conditions that might generate smaller-scale variability in thermal stress.

4.0 Results and Discussion

4.1 Reef Condition: Four Years Post-bleaching

Turf algae was the most common benthic cover type among the twenty West Hawaiʻi locations, averaging 63.1 ± 1.5% cover (Table 5), which was nearly identical to the turf cover observed in 2017 (63.7 ± 1.3%). Mean coral cover across the survey area was also similar at 19.6 ± 1.6% in 2019 compared to 18.5 ± 1.4% in 2017. A marginally significant difference in coral cover was found between depths (paired t-test; $T_{19}=1.74$, $p=0.099$), with coral cover at shallow (22.1 ± 2.3%) greater than that at deep (17.0 ± 2.2%) sites. Twenty-seven coral species were identified, and as in previous survey years, *Porites lobata* (lobe coral) and *P. compressa* (finger coral) were the most abundant, accounting for over 91% of all coral observations. *P. monticulosa* (plate and knob coral) and *Montipora capitata* (rice coral) were the next most abundant, but together accounted for only about 5% of coral observations. Other coral species were rarely encountered, with 15 species appearing only during the specialized coral health surveys (Table 5).

Average coral disease prevalence across the survey area (3.8 ± 0.5%) in 2019 was within the range of disease prevalence observed since 2015 (2.5-5.9%) (Minton *et al.* 2018b). Disease prevalence was significantly higher and more variable at shallow (5.9 ± 0.7%) compared to deep (2.3 ± 0.3%) sites (paired t-test; $T_{19}=3.07$, $p=0.006$). Five coral diseases were identified, including (most to least prevalent): *Porites* Tissue Loss Syndrome (PorTLS), *Porites* Growth Anomalies (PorGA), *Pocillopora* Tissue Loss Syndrome (PocTLS), *Porites* Trematodiasis (PorTrem) and *Montipora* Growth Anomalies (MonGA) (Table 6).

In addition to the five diseases, two other compromised heath conditions were common: algal overgrowth (ALOG) and bleaching. ALOG, primarily caused by red filamentous turf algae affected 7.3 ± 0.6% of all colonies. Bleaching prevalence in 2019 was high as the islands were experiencing prolonged high sea surface water temperatures during the time of the surveys; bleaching prevalence was 22.8 ± 1.8% at the time of the surveys. While the bleaching prevalence was 2-4 times that observed in 2016 and 2017 (Minton *et al.* 2018a, Minton *et al.* 2018b), it was a third of that observed during the 2015 mass bleaching event (64.2 ± 2.7%; Maynard *et al.* 2016). Severe bleaching, defined as the percent of colonies with >50% loss of pigmentation, was even less common in 2019 (4.5 ± 0.6%), measuring less than a tenth of that observed in 2015 (51.0 ± 3.6%; Maynard *et al.* 2016). Prevalence of bleaching varied among species, with only ~12% of *Porites lobata* colonies affected (Table 7) compared to 72% of all *Montipora capitata* colonies affected, including over a quarter showing severe bleaching. This general pattern is consistent with the expected response based on documented genera-specific bleaching susceptibility (Swain *et al.* 2016).

Coral cover at the survey sites significantly decreased between 2015 and 2016 and has not shown significant recovery at either depth (Figure 3; ANOVA, $F_{3,24}=20.78$, $p<0.001$). However, coral cover has not continued to decline, suggesting the reef condition has at least stabilized following the initial wave of coral mortality associated with the 2015 mass coral bleaching event. Coral are slow growing organisms (Minton 2015), but the lack of a detectable increase in coral cover is

Table 5. Mean (±SEM) percent cover of major benthic groups/species in 2019. An * indicates the species was observed during the coral health surveys, but was sufficiently rare to avoid detection in benthic photographs.

	West Hawai‘i	**SHALLOW**	**DEEP**
Coral	19.6 ± 1.6	22.1 ± 2.3	17.0 ± 2.2
Porites lobata	15.2 ± 1.5	19.7 ± 2.0	10.7 ± 1.7
Porites compressa	2.7 ± 0.6	1.4 ± 0.7	4.0 ± 1.0
Porites monticulosa	0.9 ± 0.9	<0.1	1.8 ± 1.7
Montipora capitata	0.2 ± 0.1	0.2 ± 0.1	0.3 ± 0.1
Porites rus	0.1 ± 0.1	0.3 ± 0.2	<0.1
Porites evermanni/lutea	0.1 ± 0.1	0.2 ± 0.2	<0.1
Pavona varians	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Montipora patula	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Pavona duerdeni	<0.1	0.1 ± 0.1	<0.1
Pocillopora meandrina	<0.1	<0.1	<0.1
Leptastrea purpurea	<0.1	<0.1	*
Psammocora nierstraszi	<0.1	*	<0.1
Leptastrea transversa	<0.1	*	<0.1
Fungia scutaria	*	*	*
Porites bernardi	*	*	*
Porites brighami	*	*	*
Porites sp.	*	*	*
Psammocora haimeana	*	*	*
Psammocora stellata	*	*	*
Cyphastrea ocellina	*	*	0
Leptastrea bewickensis	*	*	0
Montipora flabellata	*	*	0
Montipora incrassata	*	*	0
Porites annae	*	*	0
Pavona maldivensis	*	*	0
Pocillopora damicornis	*	*	0
Leptoseris incrustans	*	0	*
Porites solida	*	0	*
Turf	63.1 ± 1.5	64.8 ± 2.4	61.5 ± 1.8
Crustose Coralline Algae	8.2 ± 1.0	7.7 ± 1.3	8.6 ± 1.7
Cyanobacteria	0.2 ± 0.1	0.1 ± 0.1	0.2 ± 0.1
Other	0.2 ± 0.1	0.1 ± 0.1	0.2 ± 0.1
Macroalgae	<0.1	<0.1	<0.1
Abiotic	8.7 ± 1.1	5.2 ± 0.7	12.3 ± 1.8
Sand	6.8 ± 0.9	4.6 ± 0.7	9.1 ± 1.6
Rubble	1.9 ± 0.5	0.5 ± 0.1	3.2 ± 0.9
Recently Dead Coral	<0.1	<0.1	<0.1
Pavement	<0.1	<0.1	<0.1

Table 6. Prevalence of disease (red) and other compromised health conditions (blue) in 2019, with locations arranged from the most northerly (top) to the most southerly (bottom). Disease is the total prevalence of all diseases (% of colonies showing at least one disease). The column values for the five identified diseases (*e.g.*, PorGA) are prevalence for the described genera (% of *Porites*/*Montipora*/*Pocillopora* colonies). Bleaching is the percent of colonies fully- or partially-bleached. Severe bleaching is the percent of colonies with >50% loss of pigmentation. See text for definitions of the disease abbreviations.

	Shallow									Deep								
Site	Disease	PorGA	MonGA	PorTLS	PocTLS	Por Trem	ALOG	Bleach	Sev. Bleach	Disease	PorGA	MonGA	PorTLS	PocTLS	Por Trem	ALOG	Bleach	Sev. Bleach
Kailapa	1.0	1.0	0	0	0	0	9.0	9.7	3.8	4.6	4.4	0	6.4	0	0.3	2.9	31.3	6.4
Kawaihae	0.5	0.3	0	0.6	0	0	5.0	20.2	4.7	2.4	0	0	8.1	0	0	6.2	27.1	4.7
‘Ōhai‘ula	1.4	0.3	0	0.8	0	0	11.8	27.0	5.3	0.8	6.7	0	0	0	0	22.6	40.4	1.1
Kauna'oa	1.9	1.5	0	2.2	0	0	4.0	26.1	6.9	1.3	0	0	1.6	0	0	4.1	32.9	8.3
Kanekanaka Pt.	6.0	1.1	0	17.7	0	1.2	12.6	23.6	1.7	2.0	0.2	0	7.6	0	0	6.3	40.2	3.3
Puakō	4.5	3.9	0	3.3	0	0.7	3.7	19.9	0.3	3.9	1.6	0	9.9	0	0	9.7	43.9	4.1
Keanapukalua	9.8	10.3	0	4.0	0	0	8.3	13.6	2.1	1.6	2.0	0	0.8	0	0	5.8	17.4	4.0
Lulahala Pt.	9.3	7.8	0	7.8	0	2.9	5.7	17.7	5.9	2.2	0	0	6.8	0	0.9	5.2	28.6	8.7
Kapalaoa	7.4	6.7	0	1.1	0	0	11.3	19.4	5.6	1.6	1.4	0	0	0	0	6.0	13.9	6.4
Keawaiki	2.0	1.9	0	0.5	0	0	14.6	8.9	2.2	0.3	0	0	0.1	0	0	1.8	15.2	4.5
Laehou	0.6	0.1	0	5.1	0	0.2	5.0	32.2	10.0	1.3	0.2	0	2.7	37.5	0	3.3	33.2	5.7
Kīholo	6.1	1.0	0	6.7	0	0	14.1	16.6	1.2	1.4	1.1	0	2.0	0	0.2	9.5	31.8	4.8
Kalaemanō	7.0	1.6	0	10	0	0	7.5	11.9	2.8	2.0	0	0	2.5	0	0	4.4	19.3	1.5
Keonenui	6.5	4.3	0.4	13.2	0	0	8.8	47.7	10.2	1.8	0.4	0	1.6	0	0	7.3	32.4	3.4
Kumukea	1.5	0	0	1.5	0	0	4.0	17.4	3.7	1.2	0	0	1.6	0	0	3.9	34.5	6.5
Manini'ōwali	10.9	0.4	0	13.6	0	0	8.7	12.1	1.4	3.4	0.4	0	5.9	0	0	5.4	30.7	0.6
Makalawena	7.4	3.0	0	8.4	0	0	7.7	16.7	4.9	4.3	1.2	0	2.9	0	0	5.2	16.9	2.1
Mākole‘ā	5.1	3.9	0	3.8	0	1.7	6.5	14.5	8.9	4.2	1.4	0	4.7	0	0	8.7	34.6	7.5
Honokōhau	8.8	9.0	0	0	0	2.3	3.8	5.3	1.8	4.8	5.1	0	0	0	3.3	3.2	5.2	2.9
Keauhou	5.5	4.4	0	2.6	0	1.4	11.0	13.2	6.1	2.3	2.8	0	0	0	0	5.6	8.5	5.9

Table 7. Percent of colonies of the five most common coral species observed during the coral health surveys (>100 colonies) that were bleached and severely bleached (>50% of the colony bleached).

Species	Total Colonies	% Bleached	% Sev. Bleached
Porites lobata	9531	11.9	1.4
Porites compressa	4033	25.6	3.3
Montipora capitata	1325	72.0	26.8
Pavona varians	682	23.2	2.8
Montipora patula	434	37.1	4.1

concerning after four years, a time period during which even a recruit of a slow-growing species such as *P. lobata* should have obtained a diameter of 3-4 cm, equivalent to approximately 0.1% percent cover.

While on average, coral cover on West Hawai‘i has not increased since the 2015 mass bleaching event, some sites have shown increases. About half of the sites showed increases (Figure 4), with the deep site at ‘Ōhai‘ula showing the largest relative increase. This large increase is curious, however, especially considering most of this change occurred between 2016 and 2017 (data not shown), suggesting

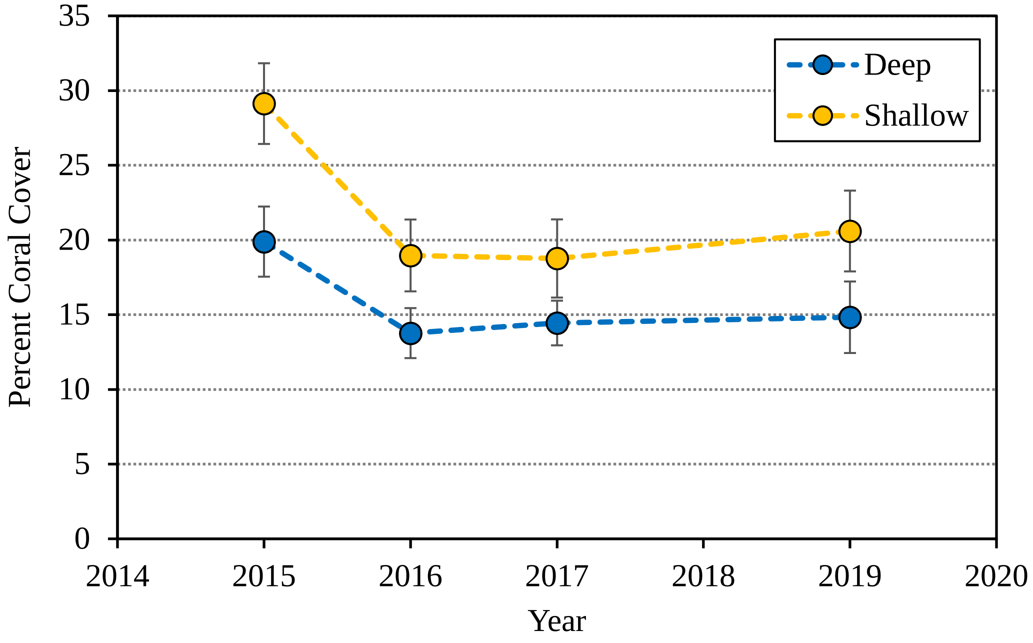

Figure 3. Mean (±SEM) percent coral cover at shallow (gold) and deep (blue) sites between 2015 and 2019. Values were derived from the reduced data set ($n_{shallow}$=13; n_{deep}=15), so annual points may vary slightly from values reported elsewhere in this and prior reports that are derived from the full data set.

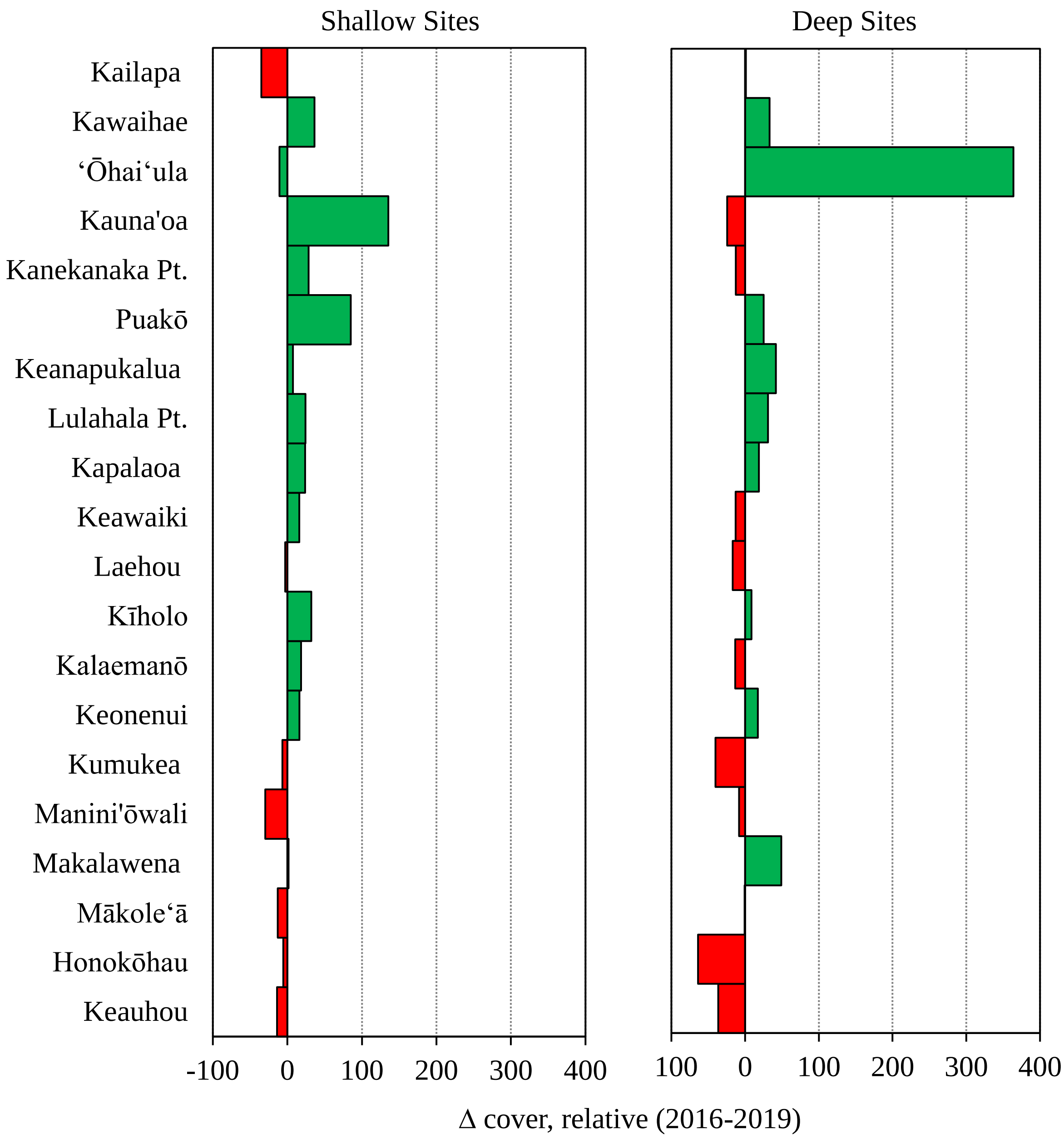

Figure 4. Relative change in coral cover between 2016 and 2019 at 20 shallow (left) and 20 deep (right) sites on West Hawai‘i. Red bars represent a decrease in cover and green bars an increase in cover between 2016 and 2019. Sites are arranged from most northerly (top) to most southerly (bottom).

the 2016 estimate might have underreported the actual coral cover. No clear spatial pattern to recovery was observed, although it is possible that more northerly shallow sites are experiencing greater recovery than more southerly ones.

Equally concerning is what appears to be a decrease in coral recruitment (Figure 5; ANOVA, $F_{3,24}$=12.67, p<0.001) especially at deep sites, where average recruitment in 2019 was half that of 2015, and has been on a declining trend since. At shallow sites, recruitment did not change in the two years following the mass coral bleaching event, but was significantly lower in 2019, declining by almost 45% relative to 2015. Given that small corals would be considered recruits over multiple survey periods due to their slow growth rates, these declining numbers suggest that recruit mortality exceeds new settlements[6]. While high recruit mortality is not surprising, it is unclear if the recruitment deficit is the result of an elevated mortality rate or a decrease in settlement, which can result in numerous ways, including reduced larval supply[7] to West Hawaiʻi reefs and/or a decrease in the rate of successful settlement[8].

Estimating coral recruitment has several challenges, and it is possible that use of different surveyors between years could account for the some of the annual differences in recruitment. However, many of the surveyors were the same between years, and all were similarly trained. An examination of the coral recruit size information also indicates that all surveyors were consistently locating even small corals (down to 1 cm), so the potential variability from surveyors does not adequately explain the trend. The declining trend in coral recruitment developing on West Hawaiʻi reefs raises concerns and warrants deeper investigation to understand and, as necessary, mitigate the cause(s).

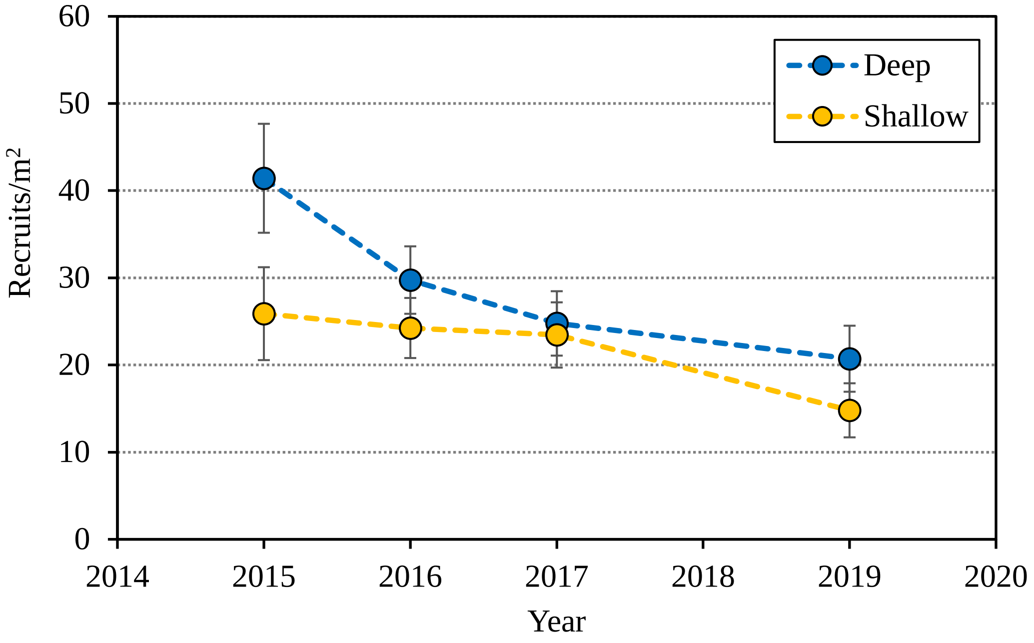

Figure 5. Mean (±SEM) density of coral recruits (colonies <5 cm) at shallow (gold) and deep (blue) sites between 2015 and 2019. Values were derived from the reduced data set ($n_{shallow}$=13; n_{deep}=15), so annual points may vary slightly from values reported elsewhere in this and prior reports that are derived from the full data set.

---

[6] Some recruits may also "grow out of" the recruit category, but data suggest this is likely a small percentage (<9%).

[7] This can occur, for example, from fewer reproductive adults or decreased fecundity in corals that survived the 2015 mass bleaching event.

[8] This can be due to reduced suitability in benthic conditions, *e.g.*, an increase in turf or unconsolidated substratum.

Coral densities showed a significant increase from 2016 to 2017, but returned to the pre-2017 levels in the most recent survey round (Figure 6; ANOVA, $F_{3,24}$=20.87, $p<0.001$), suggesting the 2017 density estimates may have been a sampling artifact. Coral colony densities appear to have

number of colonies suffering partial mortality as opposed to the outright colony death[9]. This also would be consistent with a large proportion of the coral assemblage being comprised of *P. lobata*, a species coral that has shown resistance to thermal stress and bleaching, but which is also prone to partial mortality.

As with percent cover, the changes in coral colony densities from 2016 to 2019 were highly variable among sites (Figure 7). Unlike percent cover, however, there appeared to be a spatial pattern to the recovery, with more northerly sites in the survey area showing increases in colony density and more southerly sites tending to show decreases. This trend was the reverse of that noted between 2015 and 2016, when northerly sites showed a decrease in coral colony densities and southerly sites showed increases. The change in coral density between 2015 and 2016 was correlated with bleaching prevalence and losses were assumed to be the result of bleaching related mortality (Minton *et al.* 2018a).

The composition of the benthic assemblage changed little between 2017 and 2019, with nearly identical cover of coral, crustose coralline algae (CCA), macroalgae, and other (turf and abiotic).

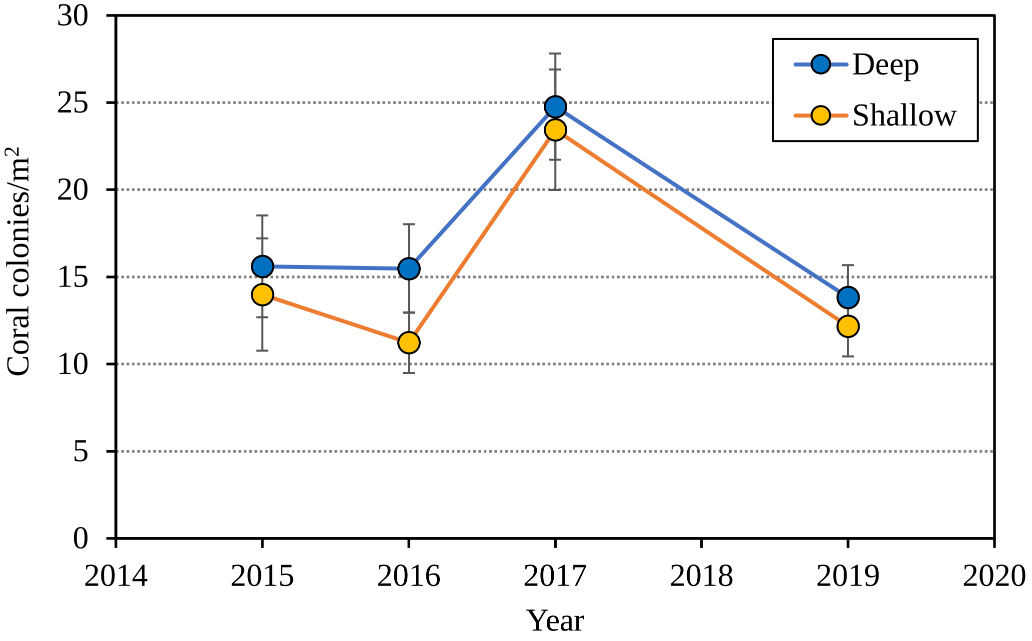

Figure 6. Mean (±SEM) density of coral colonies at shallow (gold) and deep (blue) sites between 2015 and 2019. Values were derived from the reduced data set ($n_{shallow}$=13; n_{deep}=15), so annual points may vary slightly from values reported elsewhere in this and prior reports that are derived from the full data set.

---

[9] This would result in a loss of coral cover, but not a decrease in coral density, which was consistent with the 2015-2016 survey data (Minton *et al.* 2018a)

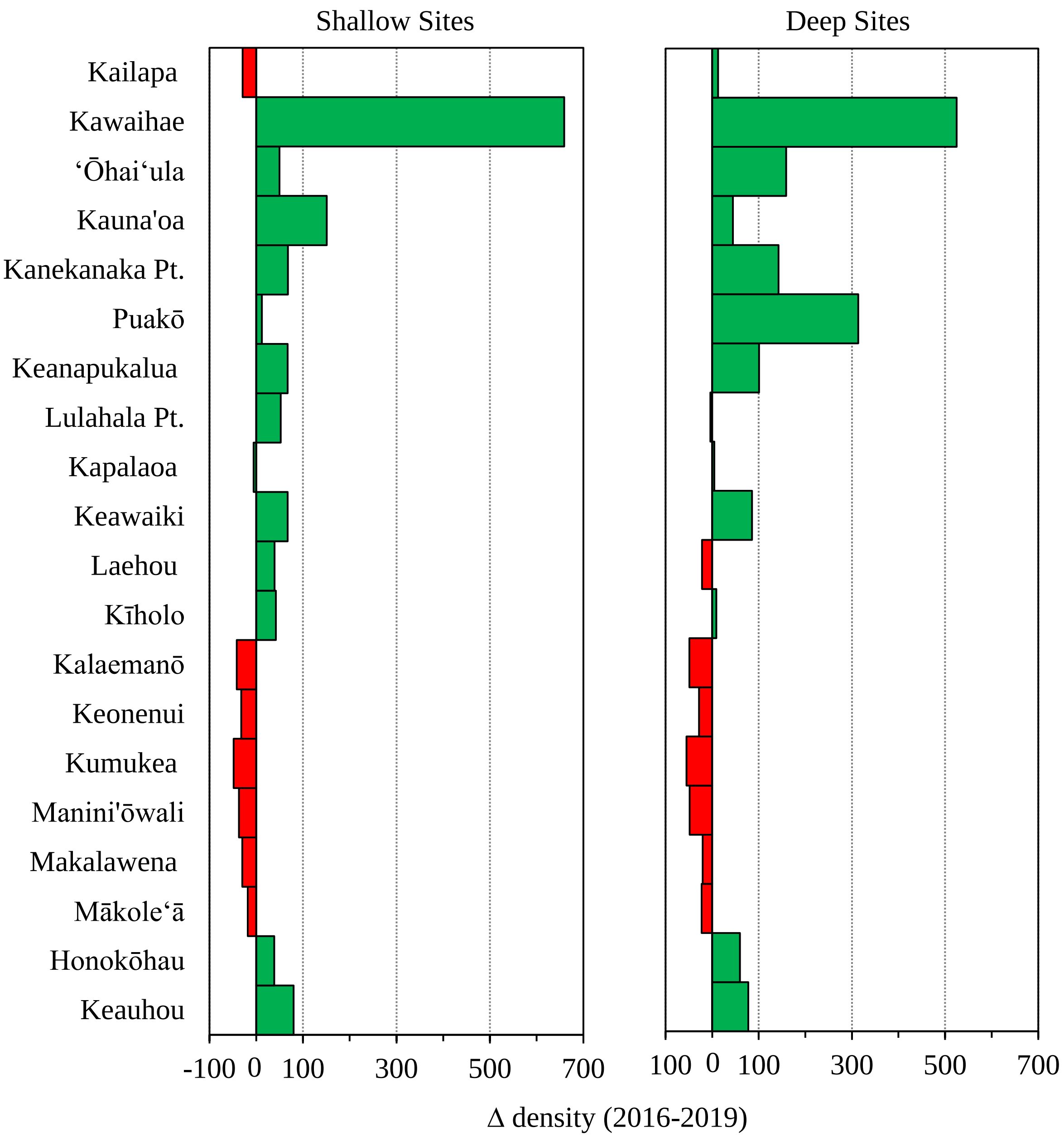

Figure 7. Relative change in coral colony density between 2016 and 2019 at 20 shallow (left) and 20 deep (right) sites on West Hawai‘i. Red bars represent a decrease in colony density and green bars an increase in colony density between 2016 and 2019. Sites are arranged from most northerly (top) to most southerly (bottom).

Coral losses from the 2015 mass coral bleaching event were initially offset by increases in CCA and turf algae/abiotic substratum (Minton *et al.* 2018a), but since 2017, have been offset primarily by turf and abiotic substratum (primarily sand and rubble), both of which tend to have negative effects on coral settlement (Figure 8).

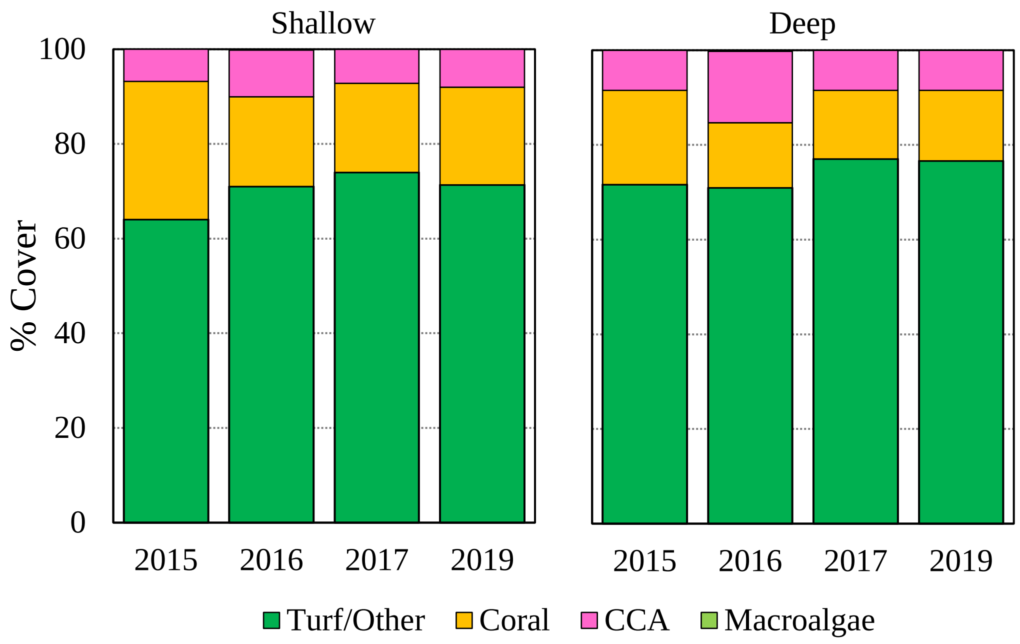

Figure 8. Mean percent cover by benthic group at shallow and deep sites along West Hawai‘i from 2015-2019. Values were derived from the reduced data set ($n_{shallow}$=13; n_{deep}=15), so annual points may vary slightly from values reported elsewhere in this and prior reports that are derived from the full data set.

A total of 117 species of reef fish in 26 families were observed across the survey area in 2019. Total fish biomass was 60.8 ± 12.7 g/m^2 and varied from a low of 14.3 ± 2.4 g/m^2 (Kawaihae) to a high of 146.0. ± 76.0 g/m^2 (Manini'ōwali). The high biomass at Manini'ōwali was driven by single whitetip shark (*Triaenodon obesus*) observed on one of the transects. These large predators are rarely observed and tend to inflate biomass values. Excluding this species lowers the Manini'ōwali biomass to 50.4. ± 12.7 g/m^2 and would make Puakō the location with the highest biomass (118.3. ± 50.5 g/m^2). Puakō and Kawaihae also had the highest and lowest biomass, respectively, in 2016 and 2017, suggesting some spatial continuity in the distribution of fish biomass on West Hawai‘i reefs.

If the shark at Manini'ōwali is ignored, the families Acanthuridae (surgeonfishes) and Scaridae (parrotfishes) contributed the most to total fish biomass, 39%, and 14% of the total, respectively (Table 8). These two families also tend to be common on many Hawaiian reefs. Herbivores accounted for 50% of the total fish biomass (Figure 9), while apex predators accounted for <1% and were rarely observed, appearing on fewer than 8% of the transects.

In 2017, total fish biomass dipped to 45.4 ± 7.2 g/m^2 (Figure 10), significantly lower than that observed in 2015 and 2016 (Minton *et al.* 2018b), but it was unclear if this decline was a product of the high annual variability typical of reef fish populations or a "real" decline. Minton *et al.* (2018b) provided additional context to interpret the 2017 decline, and concluded that while the trend appeared to be "real" it was likely the result of a "relaxation" of a spike in biomass associated with a large reef fish recruitment event that occurred in 2014. In 2019, total fish

Table 8. Mean (±SEM) fish biomass by family (g/m^2) for West Hawai‘i and by depth in 2019. Biomass was not estimated for Muraenidae (eels) due to challenges associated with accurately sizing these fish.

Family	**West Hawai‘i**	**Shallow**	**Deep**
Acanthuridae	23.8 ± 4.8	23.8 ± 4.8	23.8 ± 8.6
Scaridae	7.7 ± 1.5	7.9 ± 2.0	7.6 ± 2.3
Carcharhinidae	4.8 ± 8.4	9.6 ± 17.0	0
Balistidae	4.4 ± 0.9	6.3 ± 1.5	2.4 ± 0.7
Labridae	4.1 ± 1.2	2.7 ± 0.9	5.6 ± 2.1
Holocentridae	3.9 ± 3.2	0.6 ± 0.6	7.2 ± 6.4
Serranidae	3.2 ± 1.0	1.7 ± 1.1	4.7 ± 1.6
Mullidae	2.6 ± 1.6	3.2 ± 3.2	2.0 ± 0.8
Pomacentridae	1.5 ± 1.2	1.0 ± 0.6	2.1 ± 2.3
Chaetodontidae	1.4 ± 0.2	1.4 ± 0.3	1.4 ± 0.3
Lutjanidae	1.0 ± 0.4	0.7 ± 0.5	1.3 ± 0.7
Kyphosidae	0.6 ± 0.6	0.5 ± 0.6	0.7 ± 1.0
Lethrinidae	0.4 ± 0.3	0.1 ± 0.1	0.8 ± 0.7
Monacanthidae	0.3 ± 0.3	0	0.6 ± 0.7
Carangidae	0.3 ± 0.3	0.3 ± 0.3	0.3 ± 0.4
Diodontidae	0.2 ± 0.2	0	0.4 ± 0.4
Zanclidae	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.1
Cirrhitidae	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.1
Tetraodontidae	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Pomacanthidae	0.1 ± 0.1	<0.1	0.1 ± 0.1
Fistulariidae	0.1 ± 0.1	0.1 ± 0.2	0
Synodontidae	<0.1	0.1 ± 0.1	0
Ostraciidae	<0.1	<0.1	<0.1
Aulostomidae	<0.1	<0.1	<0.1
Blenniidae	<0.1	<0.1	<0.1
Muraenidae	Present	Present	Present
Grand Total	**60.8 ± 12.7**	**60.3 ± 19.9**	**61.4 ± 16.5**

biomass was significantly greater than in 2017 (ANOVA, $F_{3,24}$=13.73, p<0.001), and was no longer significantly different from 2016, but still lower than that observed in 2015. This fluctuation of the total fish biomass suggests that Minton *et al.*'s (2018b) conclusion may be incorrect, and the differences among survey years may be associated with annual variability. Long-term declines in reef fish populations have been documented for some West Hawai‘i reefs (Minton *et al.* 2012, 2015, 2018c,Walsh *et al.* 2013), so a regional trend should not be ruled out, but given the high temporal variability in the data, a longer timeseries will be needed to identify it.

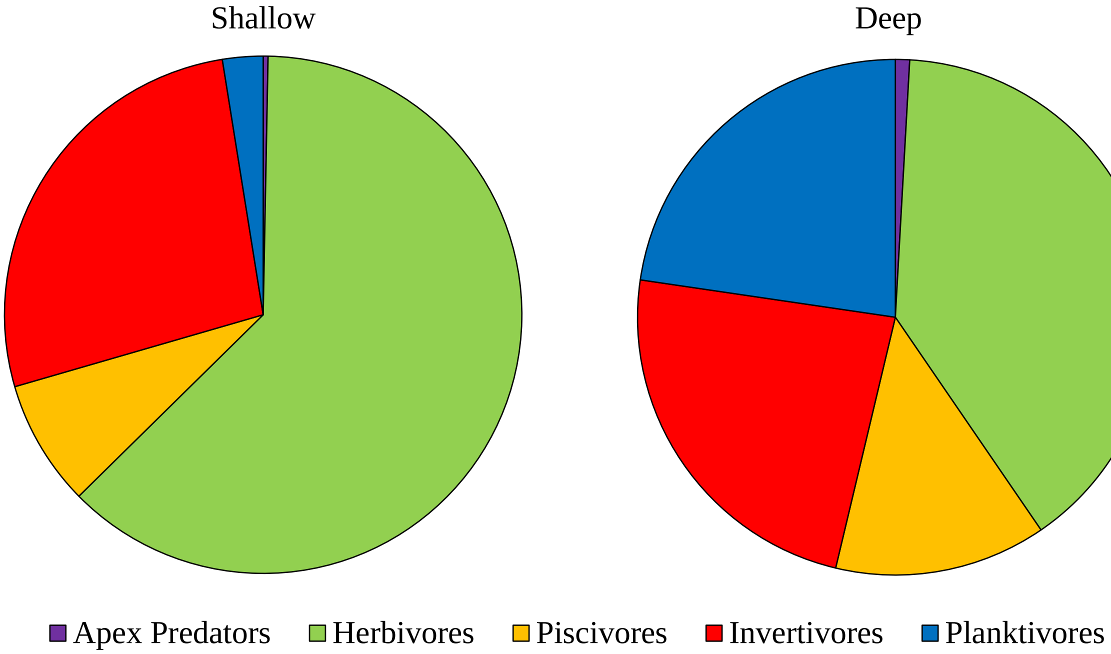

Figure 9. Trophic structure at shallow and deep sites along West Hawaiʻi in 2019.

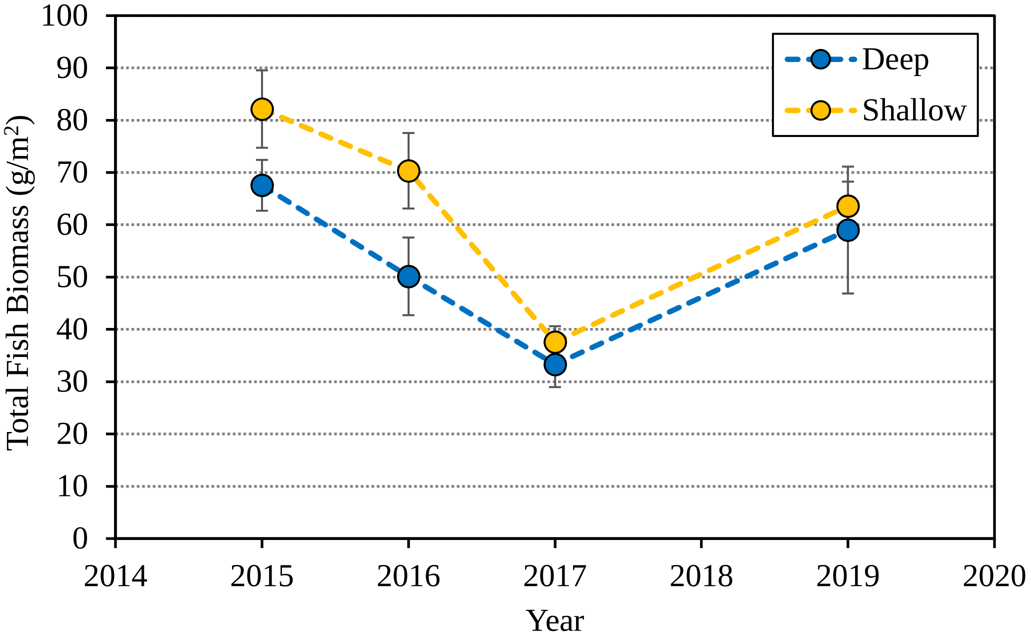

Figure 10. Mean (±SEM) total fish biomass across at shallow (gold) and deep (blue) sites between 2015 and 2019. Values were derived from the reduced data set ($n_{shallow}$=13; n_{deep}=15), so annual points may vary slightly from values derived from the full data set for a given year.

4.2 Revisiting 2015 Reef Resilience Rankings

In 2015, TNC developed rankings for the relative resilience potential for both deep and shallow sites at 20 locations in West Hawaiʻi. These rankings ordered sites by estimated resilience potential, from most resilient (rank 1) to least resilient (rank 20). The 2015 and 2019 mass coral bleaching events on West Hawaiʻi provide a unique opportunity to assess the performance of these rankings.

Sites ranked as most resilient should experience fewer and/or recover more quickly from adverse effects from bleaching events. While little recovery across the West Hawaiʻi coast has been detected as of 2019, it should still be possible to assess the effectiveness of the 2015 rankings in predicting the potential resilience of a site because of the spatial variability in the response of reefs to the event (see Figures 4 and 7). Table 9 summarizes the two measures of resistance and one measure of recovery chosen to measure a site's resilience, including their hypothesized relationship with the rankings developed in 2015.

Overall, the reef resilience rankings proved to be poor predictors for all resistance and recovery measures. In most cases, no significant correlation was found between the rankings and the measures, although a marginally significant relationship was found between the unweighted rankings at shallow sites and their change in coral cover from 2015-2016. In the other cases where a significant relationship was identified, the direction of the relationship ran counter to what would be expected if the rankings were performing as intended. For example, both the weighted and unweighted rankings were significantly correlated with the bleaching prevalence in 2019 at deep sites (Table 9), but instead of higher ranked (=more resilient) sites having lower bleaching prevalence than lower ranked (=less resilient) sites in 2019 (*i.e.*, a positive correlation), the opposite was observed (Figure 11).

4.3 Investigating Alternative Approaches to Rank Calculations

The overall poor correlation of both the unweighted and weighted 2015 reef resilience rankings with a suite of resistance and recovery measures suggests this approach to rankings is not performing as expected. While the selected measures of resistance and recovery were the best available, it is possible other measures may better represent a site's resilience. Ideally, any measure should be: 1) strongly correlated with the site's resilience, 2) straight-forward to interpret, and 3) easily measured. Assuming our measures are appropriate, the impressive data set that has been collected since 2015 should allow for a straight-forward determination of the "best" combination and weightings of indicators to generate resilience rankings. Unfortunately, two primary challenges have hampered TNC's effort.

First, most statistical approaches used to determine the appropriate indicators and their weightings require *a priori* knowledge of the resilience ranking. With this information, the variables collected in 2015 would then be assessed to determine the "best" combination and weighting of indicators that would produce the "known" rankings. These rankings could then be "tested" against their ability to predict the response of the sites to a future event at the same sites or applied to a separate set of sites for a validation test.

Table 9. Correlations of the 2015 unweighted (r) and weighted (r_{wp} and r_{ws}) reef resilience rankings with indicators of resistance and recovery for 20 shallow and 20 deep sites on West Hawai‘i. Correlations were conducted using the reduced dataset. ns=not significant, *=0.05<p<0.1; **=p<0.05.

	Shallow	Deep	Hypothesis
Resistance			
1. Relative Change in Coral Abundance (2015-2016)			
Δ coral cover, relative[†]	$r = -0.412^{*}$ $r_{wp} = -0.398^{ns}$ $r_{ws} = -0.404^{ns}$	$r = 0.137^{ns}$ $r_{wp} = 0.123^{ns}$ $r_{ws} = 0.138^{ns}$	(-) correlation
Δ coral colony density, relative	$r = -0.353^{ns}$ $r_{wp} = -0.370^{ns}$ $r_{ws} = -0.396^{ns}$	$r = 0.158^{ns}$ $r_{wp} = 0.110^{ns}$ $r_{ws} = 0.038^{ns}$	(-) correlation
2. Response to 2019 Bleaching Event			
% tissue bleached	$r = -0.021^{ns}$ $r_{wp} = -0.002^{ns}$ $r_{ws} = -0.010^{ns}$	$r = -0.282^{ns}$ $r_{wp} = -0.213^{ns}$ $r_{ws} = -0.103^{ns}$	(+) correlation
bleaching prevalence	$r = -0.052^{ns}$ $r_{wp} = -0.017^{ns}$ $r_{ws} = -0.034^{ns}$	$r = -0.507^{**}$ $r_{wp} = -0.480^{*}$ $r_{ws} = -0.434^{ns}$	(+) correlation
Recovery			
1. Relative Change in Coral Abundance (2016-2019)			
Δ coral cover, relative	$r = -0.222^{ns}$ $r_{wp} = -0.223^{ns}$ $r_{ws} = -0.155^{ns}$	$r = -0.036^{ns}$ $r_{wp} = -0.020^{ns}$ $r_{ws} = 0.042^{ns}$	(-) correlation
Δ coral colony density, relative	$r = 0.321^{ns}$	$r = 0.337^{ns}$ $r_{wp} = 0.365^{ns}$	(-) correlation

$r_{wp} = 0.327^{ns}$ $r_{ws} = 0.406^{ns}$

$r_{ws} = 0.392^{ns}$

[†] See footnote 4, page 13 for more information on relative cover.

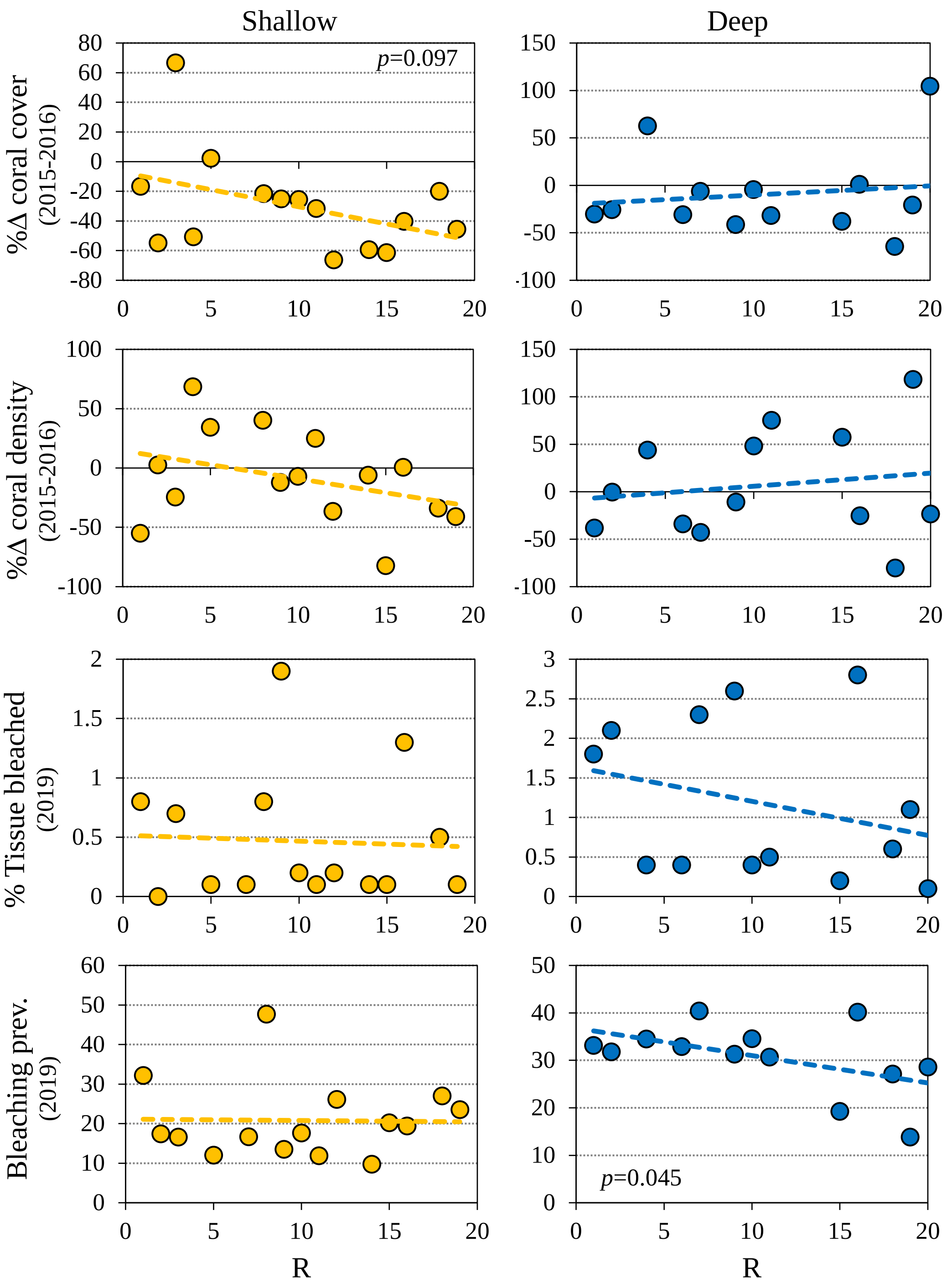

Figure 11. Four indicators of resistance and two indictors of recovery (next page) vs. unweighted 2015 reef resilience ranks (R) at 15 shallow (gold) and 13 deep (blue) sites on West Hawai‘i. Lines are only intended to help visualize the general trend in the data and do not indicate a significant relationship. P-values are provided only for significant correlations, but see Table 9 for a full summary of the indicators and results.

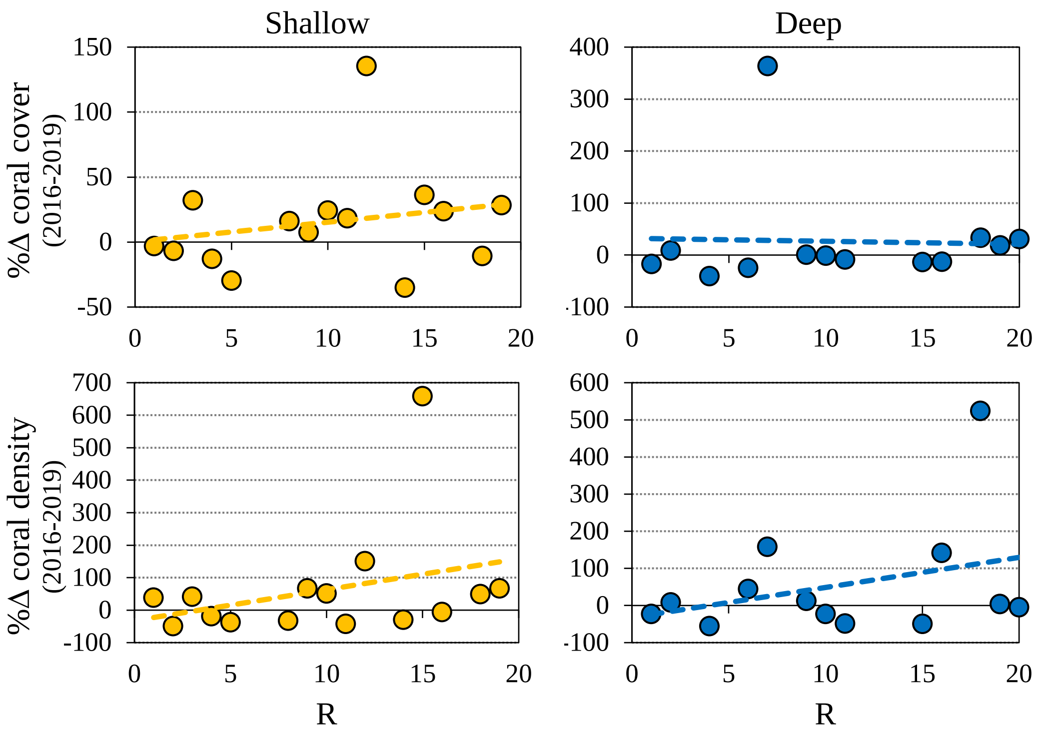

Figure 11 (con't). Four indicators of resistance (previous page) and two indictors of recovery vs. unweighted 2015 reef resilience ranks at 15 shallow (gold) and 13 deep (blue) sites on West Hawai‘i. Lines are only intended to help visualize the general trend in the data and do not indicate a significant relationship. P-values are provided only for significant correlations, but see Table 6 for a full summary of the indicators and results.

Attempts were made to use the three measures of resilience (see Table 9 for the measures and their predicted relationship with the resilience ranks) to assign rankings to the shallow and deep sites so that we could apply this approach. However, initial attempts to assign resilience rankings to the sites proved intractable. Ordinating the data (*i.e.*, a Principle Component Analysis) using either the cover-specific or colony-specific measures produced PCA-axes that were difficult to cleanly interpret (*e.g.*, Figure 12). Sites also did not cluster, so ranking sites or grouping them into qualitative categories (*e.g.*, high medium, low) would have been subjective, and while sites showed a somewhat linear arrangement in ordination space, it was not clear how their position in space was related to their overall resilience due to the incongruence of the interpretation of the axes. These difficulties arose because many sites showed contradictory relationships for resistance and recovery (Table 10). Sites that showed high relative resilience (low rank number in Table 10) often would show low relative recovery (high rank number in Table 10). In addition, we found little consistency between the cover- and colony-specific measures of resilience, which was especially apparent at deep sites.

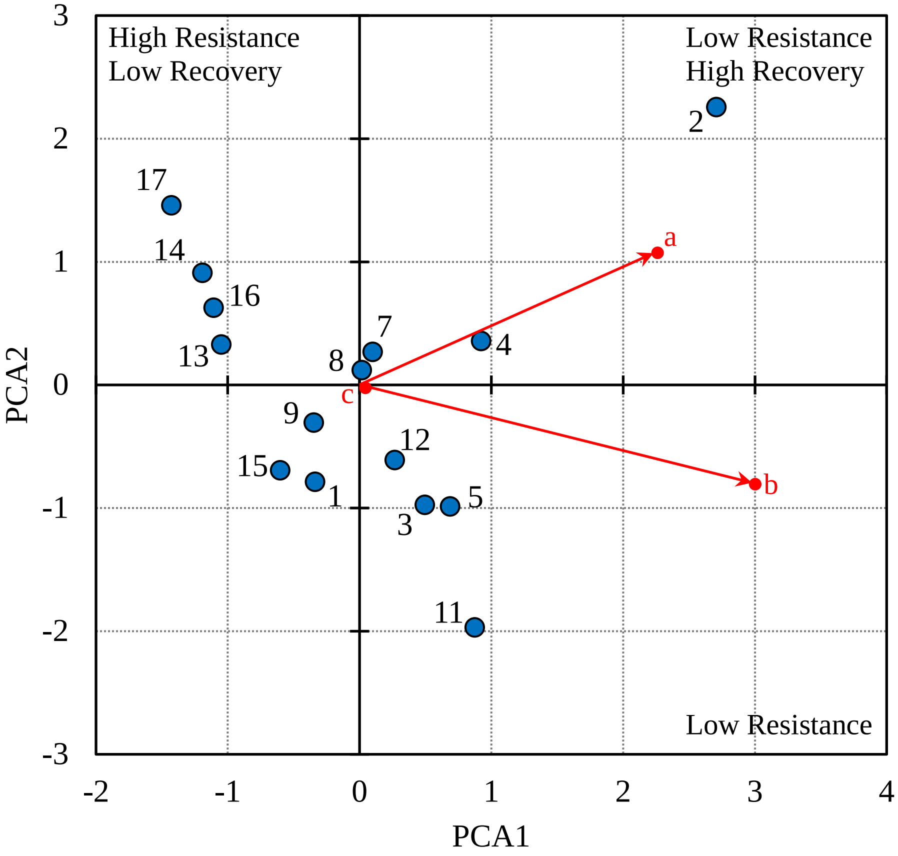

Figure 12. An example ordination of results from a principle components analysis of deep sites using colony-specific measures of resistance and recovery. Analysis was conducted using the reduced data set (n_{deep}=15) that had been normalized. The numbers next to the blue points correspond with those in Table 10. Red arrows and points show the direction and magnitude of (a) the relative change in coral density from 2016-2019, (b) the relative change in coral density from 2015-2016, and (c) the bleaching prevalence in 2019. Text in the corners of the Figure describes qualitatively the likely resistance and recovery that would place a site within that quadrant. Where no text is provided, the likely resistance and recovery as unclear. Ordination results for shallow sites and cover-specific measures are similar and have not been shown.

The difficulties encountered trying to identify resilient sites on West Hawai‘i highlight the second challenge: the understanding of resilience in marine ecosystems is still in its nascent phase. While coral reef resilience as an applied ecological concept has been operationalized primarily through designing managed areas networks based on resilience principles and assessing the resilience of coral reef locations, the science of resilience remains primarily theoretical (*e.g.*, Mumby 2009). How to translate these theoretical concepts into measurable indicators is a non-trivial challenge, especially given the complexities of ecological communities that arise as a result of their diversity and the myriad of interactions that occur across multiple spatial and temporal scales and among biological, physical and chemical components of the

Table 10. Shallow and deep (next page) sites ranked by their resistance (blue) and recovery (green) measures. Mean rank was calculated by first averaging the ranks for the two resistance measures, and then averaging with the recovery measure. While all sites are included in the table, ranks were determined from the reduced dataset (see methods more information). Sites are arranged from the most northerly (top) to most southerly (bottom). Numbers for deep sites correspond to those in Figure 12.

	Cover-Specific Measures				**Colony-Specific Measures**			
	Δ Cor. Cover (2015-2016)	%Tissue BL (2019)	Δ Cor. Cover (2016-2019)	Mean Rank	Δ Cor. Den. (2015-2016)	Prev. BL	Δ Cor. Den. (2016-2019)	Mean Rank
Shallow Sites								
Kailapa	2	9	5	5.25	7	1	10	7
Kawaihae	6	7	4	5.25	15	10	1	6.75
‘Ōhai‘ula	10	15	7	9.75	11	13	6	9
Kauna'oa	3	8	12	8.75	12	12	2	7
Kanekanaka Pt.	11	4	15	11.25	13	11	4	8
Puakō								
Keanapukalua	4	14	14	11.5	9	4	3	4.75
Lulahala Pt.	15	6	8	9.25	8	8	5	6.5
Kapalaoa	14	13	9	11.25	6	9	9	8.25
Keawaiki								
Laehou	9	11	11	10.5	14	14	8	11
Kīholo	7	10	3	5.75	10	5	7	7.25
Kalaemanō	12	2	10	8.5	4	2	14	8.5
Keonenui	8	12	1	5.5	2	15	12	10.25
Kumukea	5	1	6	4.5	5	7	15	10.5
Manini'ōwali	13	5	13	11	3	3	13	8
Makalawena	1	3	2	2	1	6	11	7.25
Mākole‘ā								
Honokōhau								
Keauhou								

Table 10 (con't). Shallow (previous page) and deep sites Rank by their resistance and recovery measures. Mean rank was calculated by first averaging the ranks for the two resistance measures, and then averaging with the recovery measure. While all sites are included in the table, ranks were determined from the reduced dataset (see methods more information). Sites are arranged from the most northerly (top) to most southerly (bottom). Numbers for deep sites correspond to those in Figure 12.

	Cover-Specific Measures				**Colony-Specific Measures**			
	Δ Cor. Cover (2015-2016)	%Tissue BL (2019)	Δ Cor. Cover (2016-2019)	Mean Rank	Δ Cor. Den. (2015-2016)	Prev. BL	Δ Cor. Den. (2016-2019)	Mean Rank
Deep								
1. Kailapa	8	12	11	10.5	9	6	5	6.25
2. Kawaihae	11	10	13	11.75	12	3	1	4.25
3. ‘Ōhai‘ula	12	7	9	9.25	13	13	2	7.5
4. Kauna'oa	10	3	5	5.75	10	8	4	6.5
5. Kanekanaka Pt.	9	13	1	6	11	12	3	7.25
Puakō								
Keanapukalua								
6. Lulahala Pt.	13	1	2	4.5	8	4	8	7
7. Kapalaoa	4	8	12	9	1	1	6	3.5
Keawaiki								
8. Laehou	2	9	7	6.25	7	9	10	9
9. Kīholo	6	11	3	5.75	6	7	7	6.75
10. Kalaemanō	3	5	4	4	4	2	12	7.5
Keonenui								
11. Kumukea	1	6	10	6.75	5	10	13	10.25
12. Manini'ōwali	5	4	8	6.25	2	5	11	7.25
Makalawena								
13. Mākole‘ā	7	2	6	5.25	3	11	9	8
Honokōhau								
Keauhou								

ecosystem. Indeed, recent studies looking at the recovery dynamics of coral reefs around the world have found that which resilience drivers are most important for recovery can vary considerably between regions (Graham *et al.* 2015).

Reef resilience assessments are intended to aid managers by identifying reefs that are likely to undergo a change in their "state" as a result of a stressor or stressors (*i.e.*, are or are not resilient), allowing for the more effective use of limited resources through the better targeting of the types and locations of management actions. Resilience assessments are based on our current understanding and subsequent measurement of coral reef characteristics, processes, and responses to stressors, with the intention that these indicators are correlated with an ecosystem's ability to resist and/or recover. Based on available data, coral reef scientists have identified a suite of 61 reef resilience indicator variables (see McClanahan *et al.* 2012 for a discussion). This list includes variables that address species community composition, species tolerances, demographics ecological processes and information on stressors. For West Hawaiʻi, we selected a subset of primarily biological indicators to construct our resilience rankings, incorporating almost all of "top" the indicators recommended by McClanahan *et al.* 2012. It may be that the subset selected excluded important factors and processes influencing the resilience of our study locations. These unaccounted for variables may be inhibiting our ability to develop rankings that accurately predict the resistance and recovery at our sites, and it may be that a more inclusive or refined suite of indicators may help strengthen the resulting rankings.

Minton *et al.* (2018a) explored the relationship of variables of environmental stress to the 2015 resilience rankings and found that the 20 West Hawaiʻi locations formed three distinct clusters based on the levels and types of stress. They also noted that the resilience ranks of the sites comprising each cluster corresponded well with expectations, *e.g.*, sites with a low number of stressors tended to be ranked as more resilient. However, sites within these clusters showed a wide range of resistance and recovery with no discernable pattern. To more thoroughly investigate the potential relationship between environmental stress and a site's resistance and recovery, the three measures of resistance and recovery were correlated against the first principle component axis from the Minton *et al.* (2018a) PCA analysis. No significant relationships were found. That the environmental stress variables correlated well with the unweighted 2015 resilience rankings (Minton *et al.* 2018a) and not with measures of resistance and recovery suggests the rankings may be better indicators of general stress on these reefs than as a measure of their resilience to climate change broadly and coral bleaching specifically.

While beyond the scope of this current effort, it may fruitful to explore a wider range of potential indicators, which is conceivable given the breadth of information collected at these 20 West Hawaiʻi locations. The West Hawaiʻi reef resilience dataset encompasses multiple spatial and temporal scales and addresses information on biological composition, ecological processes (*i.e.*, coral recruitment), and stressors. In addition, there may be benefits to revisiting the approach to resilience assessments, and instead of trying to create a ranking approach that encompasses both resistance and recovery, examine these two concepts separately. The measures of resistance and recovery indicated that most of the 20 West Hawaiʻi reef locations included in this study showed better resistance or recovery, but seldom scored well in both. In hindsight, this may not be a surprising finding, given that reefs showing little resistance should incur the greatest negative effect of a climate change event, and therefore would have the largest "space" over which to recover. We have attempted to control for this by using relative measures of loss and gain, but assuming reefs were near their maximum[10] potential state prior to the 2015, reefs with high resistance would have little potential to increase in the years following the 2015 bleaching[11]. While being able to encapsulate both the resistance and recovery components of resilience into a single score can make it easier to communicate and more straightforward to apply to management decisions, these two concepts do not need to be combined into a single measure, and separating them may make the challenges illustrated above more tractable. In addition, highlighting the potential differences in resistance and recovery may not only shed light on the inherent differences among reefs, but may provide greater insight into the threats affecting a location's long-term persistence, and thus may improve management efforts.

---

[10] As used here, the maximum potential state, which is loosely analogous with a habitat's carrying capacity, is not assumed to be fixed and can be affected by the presence of chronic natural ecological and anthropogenic stressors. As these persistent stressors change over time, the maximum potential state for corals also changes, which affects the upper limits on the abundance and condition of a species or population. Therefore, stochastic events such as mass beaching that do not necessarily result in a permanent change to the habitat, can reduce an assemblage below its maximum potential state, with the more severe the mortality from the event, the more reduction that occurs.

[11] This would suggest that relative change in coral cover is not a good measure of recovery, and instead any measure of recovery would need to account for the assemblage’s "state" within a much broader ecological framework, including the carrying capacity of the environment and the successional stage of the community, both of which are not static.

5.0 Conclusions

Between 2015 and 2016, the reefs at 20 West Hawaiʻi locations lost ~25% (relative decline) of their coral, most likely as a result of the 2015 mass coral bleaching event. In the four years since the bleaching event, these reefs have shown little sign of recovery, and while these areas appear to have stabilized at a lower level of coral cover (~19-20%, which was down from ~25% in 2015), indications of declining coral recruitment raise concerns about the long-term condition of these reefs.

As part of this ongoing study of West Hawaiʻi reefs, reef resilience rankings were generated for the 20 locations. These rankings were intended to aid with reef management by providing information on the relative resilience of the shallow and deep reef areas at each location to assist managers with the development and implementation of conservation and mitigation actions aimed at improving reef and marine resource condition into a future heavily effect by climate change. Unfortunately, the 2015 ranking (unweighted and weighted) were not correlated with any of the measures of site resistance and recovery we examined here, suggesting the rankings as constructed are not effective at "predicting" a site's relative resilience to climate change stress, with the important caveat that while four years is a reasonable time in which to expect to see recovery, it is too short to be able to definitely address site's recovery potential. Attempts to refine the ranking approach were unsuccessful due to the limitations of the statistical methods available and our nascent understanding of the complexities associated with reef resilience. While beyond the scope of this study, the path forward may require a deconstructionist approach the resilience concept, and separate focus on the ability of reef to resist and recover from climate change events at each location. This approach may provide greater insight into to threats affecting reefs, and may improve management efforts.

6.0 Acknowledgements

These surveys would not have been possible without the generous support of many scientists from partner organizations that helped conduct the fieldwork, including researchers from NOAA (Dr. Courtney Couch, Rhonda Suka, and Rebecca Weible), the Hawaiʻi Institute of Marine Biology (Chelsie Counsell, Angela Richards Dona, Yuko Stender, and Anita Tsang), the Hawaiʻi Division of Aquatic Resources (Nathan Hayes), the University of Hawaiʻi Hilo (Jon Ehrenberg, Ashley Pugh, and Mia Lamirand), and TNC (Chad Wiggins); they all have our deepest gratitude. The authors also thank the crew at Moana 'Ohana, LLC for operations support beyond any expectation. The Hawaiʻi Division of Aquatic Resources, Dr. John Burns of University of Hawaiʻi Hilo, Kona Diving Company, and Kohala Divers provided supplies and support essential for success in the field. Finally, we thank Jeff Maynard, Mike Nakachi, Kaikea Nakachi, Alohi Nakachi, Benjy Garfinkle, Earl Kam, Preston Kainoa, Sallie Beavers, Kaikea Carlson, Amanda McCutcheon and others at the National Park Service, and the Division of Aquatic Resources staff Dr. William Walsh, Ross Martin, Lindsey Kramer, Laura Jackson, Nikki Smith, Megan Lamson and Stacia Marcoux.

Funding to support the 2019 surveys was provided by the Harold K.L. Castle Foundation and the National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Office of Habitat Conservation as administered by the Office of Habitat Conservation through award NA17NMF4630301.

7.0 References

Anthony, K. R. N. P. A. Marshall, A. Abdulla, R. Beeden, C. Bergh, R. Black, C. M. Eakin, E. T. Game, M. Gooch, N. A. J. Graham, A. Green, S. F. Heron, R. van Hooidonk, C. Knowland, S. Mangubhai, N. Marshall, J. A. Maynard, P. McGinnity, E. McLeod, P. J. Mumby, M. Nyström, D. Obura, J. Oliver, H. P. Possingham, R. L. Pressey, G. P. Rowlands, J. Tamelander, D. Wachenfeld and S. Wear. 2015. Operationalizing resilience for adaptive coral reef management under global environmental change. *Glob. Change Biol.* 21: 48-61.

Bellwood, D. R., A. S. Hoey, J. L. Ackerman and M. Depczynski. 2006. Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Glob. Change Biol.* 12: 1587-94

Cesar. H. S. and P. van Beukering. 2004. Economic valuation of the coral reefs of Hawaiʻi. *Pac. Sci.* 58: 231-42.

Chapin, F. S., G. P. Kofinas and C. Folke. 2009. *Principles of ecosystem stewardship. Resilience-based natural resource management in a changing world*. New York, NY, USA: Springer.

Friedlander, A. M. and J. D. Parrish. 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology* 224: 1-30.

Froese, R. and D. Pauly. 2011. *FishBase.* World Wide Web electronic publication. www.fishbase.org, version (06/2011).

Garpe, K. C., S. A. S. Yahya, U. Lindahl and M. C. Öhman. 2006. Long-term effects of the 1998 coral bleaching event on reef fish assemblages. *Mar. Ecol. Prog. Ser.* 315: 237-47.

Graham, N. A., D. R. Bellwood, J. E. Cinner, T. P Hughes, A. V. Norström and M. Nyström. 2013. Managing resilience to reverse phase shifts in coral reefs. *Front. Ecol. Environ.* 11: 541-8.

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

Kramer, K. L., S. P. Cotton, M. R. Lamson and W. J. Walsh. 2016. Bleaching and catastrophic mortality of reef-building corals along West Hawaiʻi island: findings and future directions. *Proc. 13th Int. Coral Reef Symp., Honolulu*: 229-241.

Maynard, J. A., S. McKagan, L. Raymundo, S. Johnson, G. N. Ahmadia, L. Johnston, P. Houk, G. J. Williams, M. Kendall, E. McCleod, D. Tracey, and S. Planes. 2015. Assessing relative resilience potential of coral reefs to inform management. *Biol. Conserv.* 192: 109-19.

Maynard, J., E. Conklin, D. Minton, R. Most, C. Couch, G. J. Williams, J. Gove, B. Schumacher, W. Walsh, J. Martinez, D. Harper, D. Jayewardene B. Parker and L. Watson. 2016. Relative resilience potential and bleaching severity in the West Hawaiʻi Habitat Focus Area in 2015. NOAA Coral Reef Conservation Program. NOAA Tech. Memorandum CRCP 26. 53 pp.

Maynard, J. A., P.A Marshall, B. Parker, E. Mcleod, G. Ahmadia, R. van Hooidonk, S. Planes, G. J. Williams, L. Raymundo, R. Beeden and J. Tamelander. 2017. A Guide to Assessing Coral Reef Resilience for Decision Support. Nairobi, Kenya: UN Environment.

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: e42884.

Minton, D. 2015. Review of Growth Rates for Indo-Pacific Corals. Report prepared for National Marine Fishery Service, National Oceanic and Atmospheric Administration. 55 pp.

Minton, D., E. Conklin, P. Weiant and C. Wiggins. 2012. 40 Years of Decline on Puakō's Coral Reefs: A review of Historical and Current Data (1970-2010). TNC Technical report prepared for the National Fish and Wildlife Foundation. 140 pp.

Minton, D., E. Conklin, A. Friedlander, R. Most, K. Pollock, K. Stamoulis and C. Wiggins. 2015. Establishing the Baseline Condition of the Marine Resources: Results of the 2012 and 2013 Ka'ūpūlehu, Hawaiʻi Marine Surveys. TNC Technical Report. 40 pp.

Minton, D., E. Conklin, C. Couch, R. Amimoto, R. Carr, H, Lynch, R. Most, and C. Wiggins. 2018a. Final Baseline Condition Assessment: 2016 West Hawaiʻi Reef Resilience Marine Surveys. TNC Technical Report. 37 pp.

Minton, D, E. Conklin, C. Couch, R. Amimoto, R. Carr, H. Lynch, R. Most, J. Rose, C. Walsh and C. Wiggins. 2018b. Evaluating Coral Reef Recovery to Improve Reef Resilience Planning Along the West Coast of Hawaiʻi Island. TNC Technical Report. 31 pp.

Minton, D., C. Couch, R. Most, C. Wiggins, and E. Conklin. 2018c. Final Baseline Condition Assessment: 2015 and 2016 Ka'ūpūlehu, Hawaiʻi Marine Surveys. TNC Technical Report. 60 pp. 61,

Mumby, P. J., A. Hastings, J. G. Edwards. 2007. Thresholds and the resilience of Caribbean coral reefs. *Nature* 450: 98-101.

Mumby, P. J. 2009. Phase shifts and the stability of macroalgalcommunities on Caribbean coral reefs. *Coral Reefs* 28:761-73.

NOAA CRW 2016. 2015 Annual Summaries of Thermal Conditions Related to Coral Bleaching for NCRMP Jurisdictions.

Swain, T. D. J. B. Vega-Perkins, W. K. Oestreich, C. Triebold, E. Dubois, J. Henss, A. Baird, M. Siple, V. Backman and L. Marcelino. 2016. Coral bleaching response index: a new tool to standardize and compare susceptibility to thermal bleaching. *Glob. Change Biol.* 22: 2475-88.

van Hooidonk, R, J. A. Maynard, D. Manzello and S. Planes. 2014. Opposite latitudinal gradients in projected ocean acidification and bleaching impacts on coral reefs. *Glob. Change Biol.* 20: 103-12.

Walsh, W., S. Cotton, C. Barnett, C. Couch, L. Preskitt, B. Tissot, and K. Osada-D'Avella. 2013. Long-Term monitoring of coral reefs of the main Hawaiian Islands. Final Report for NOAA Coral Reef Conservation Program (NA09NOS4260100). 97 pp.

Weeks, R. and S. D. Jupiter. 2013. Adaptive comanagement of a marine protected area network in Fiji. *Conserv. Biol.* 27: 1234-44.

West, J. M. and R. V. Salm. 2003. Resistance and resilience to coral bleaching: implications for coral reef conservation and management. *Conserv. Biol.* 17: 956–67.

Appendix A.

Twenty locations (shallow and deep survey sites) originally surveyed in 2015 and repeated in 2016, 2017 and 2019. See Minton *et al.* (2018a) for additional discussion of realignment and installation of the 2016 transect.

#	Location	Survey Site Lat./Long.	Notes
1	Kailapa	S: (20.05962, -155.84837) D: (20.05939, -155.84876)	North Kohala FRA
2	Kawaihae	S: (20.03571, -155.83661) D: (20.03566, -155.83714)	Near harbor
3	ʻŌhaiʻula	S: (20.02049, -155.82993) D: (20.0204, -155.8312)	Offshore of Pelekane Bay (sediment)
4	Kauna'oa	S: (20.00066, -155.82893) D: (19.99986, -155.83092)	Near golf course
5	Kanekanaka Pt.	S: (19.98635, -155.83212) D: (19.98668, -155.8338)	FRA
6	Puakō	S: (19.96976, -155.84755) D: (19.97007, -155.84764)	Puakō Bay and Puakō Reef FMA; near residential development; DAR Long-term Monitoring Site
7	Keanapukalua	S: (19.95174, -155.86589) D: (19.95194, -155.86681)	Puakō-Anaehoomalu FRA / Netting Restricted Area; near golf course; DAR Long-term Monitoring Site
8	Lulahala Pt.	S: (19.93455, -155.88426) D: (19.93513, -155.88478)	Puakō-Anaehoomalu FRA / Netting Restricted Area; near golf course
9	Kapalaoa	S: (19.91363, -155.89874) D: (19.91402, -155.9006)	Puakō-Anaehoomalu FRA / Netting Restricted Area
10	Keawaiki	S: (19.89031, -155.90777) D: (19.89013, -155.91025)	DAR Long-term Monitoring Site
11	Laehou	S: (19.87313, -155.92201) D: (19.87344, -155.92252)	
12	Kīholo	S: (19.85513, -155.93415) D: (19.85527, -155.93479)	Kīholo Bay FMA
13	Kalaemanō	S: (19.85339, -155.95826) D: (19.85392, -155.95844)	
14	Keonenui	S: (19.843, -155.98045) D: (19.84298, -155.98122)	Ka'ūpūlehu Marine Reserve; near residential development; DAR Long-term Monitoring Site

#	Location	Survey Site Lat./Long.	Notes
15	Kumukea	S: (19.83415, -155.9976) D: (19.83444, -155.99803)	Ka'ūpūlehu Marine Reserve; near hotel/resort
16	Manini'ōwali	S: (19.81315, -156.00703) D: (19.81344, -156.00761)	Kikaua Pt- Mākoleʻā Netting Restricted Area
17	Makalawena	S: (19.79692, -156.0268) D: (19.79738, -156.02708)	Kikaua Pt- Mākoleʻā Netting Restricted Area; DAR Long-term Monitoring Site
18	Mākoleʻā	S: (19.78396, -156.04752) D: (19.78407, -156.048)	
19	Honokōhau	S: (19.6722, -156.03036) D: (19.6719, -156.03117)	Kaloko-Honokōhau FRA / Netting Restricted Area; near harbor; DAR Long-term Monitoring Site
20	Keauhou	S: (19.5684, -155.96903) D: (19.56838, -155.96933)	Kailua-Keauhou FRA; near golf course; DAR Long-term Monitoring Site

Appendix B.

Survey Methods

Coral Health

Coral health and disease surveys were conducted along the first 10 m of each transect line. All coral colonies within a 1-m wide belt were identified to species and enumerated. The condition of each colony was assessed, and any signs of diseases (*i.e.*, growth anomalies, Trematodiasis, and tissue loss syndrome) and/or compromised health (*i.e.*, algal overgrowth, discoloration, bleaching or paling, physical damage, gastropod predation and crown-of-thorns predation) were noted.

Coral health was examined using disease prevalence, calculated as follows:

$$\text{Prev} = \frac{\text{\# of colonies with at least 1 type of DZ or COMP}}{\text{\# of total colonies}}$$

The prevalence of each condition for all coral or for individual species was calculated as follows:

$$\text{Prev}_{\text{(DZ or COMP)}} = \frac{\text{\# of colonies with a specific DZ or COMP}}{\text{\# of total colonies or \# of colonies of a species}}$$

Juvenile Corals

All coral colonies ≤5 cm in diameter (longest dimension) whose geometric center lay within a 0.5 x 0.5 m quadrat were counted and identified to the lowest taxonomic level. Four quadrats were haphazardly spaced ~2 m apart within the first 10 m of each transect, corresponding with coral health belt transect.

Benthic Topography (Rugosity)

The topographic complexity of the bottom at each site was estimated using an index of rugosity calculated along the first 10 meters of each transect by dividing the length of brass chain required to contour the bottom by the 10-m transect length (McCormick 1994). For this index, a value of one represents a flat surface with no topographic relief, and increasing values represent more topographically complex substratum.

Benthic Cover

At each survey site, photographs of the bottom were taken every meter along each 25-m transect line using a Canon Powershot camera or equivalent mounted on a 0.8-m PVC monopod. This generated 25 images for each survey site, with each photo covering approximately 0.8 x 0.6 m of the bottom. A 5-cm scale bar marked in 1-cm increments was included in all photographs.

Twenty randomly-selected photographs from each transect were analyzed to estimate the percent cover of coral, algae, and other benthic organisms present. As needed, selected photographs were imported into Adobe Photoshop CS5 where their color, contrast, and tone were auto-balanced to improve photo quality prior to analysis. Photos were analyzed using Coralnet, an online repository and resource for benthic images analysis maintained by the University of California San Diego (Beijbom *et al.* 2015). Thirty random points were overlaid on each digital photograph, and the benthic component under each point was identified to the lowest possible taxonomic level, primarily individual coral species, algae at higher taxonomic resolution (*e.g.*, red, green, brown, turf, and crustose coralline, but sometimes genera), and abiotic substratum type. All photographs were processed by the same analyst to reduce potential observer variability. Once completed, the raw point data from each photograph was combined to calculate the percent cover of each benthic component for the survey site.

Photo analysis is sensitive to the resolution of the photograph and often does a poor job of detecting rare coral species. In contrast, the coral health surveys, which are conducted *in situ* and entail a thorough inspection of the benthos, including within crevices, on vertical sections, and beneath overhangs (all of which are often blocked from view in photographs) are much better at locating rare and/or small species. Therefore, coral species richness was determined using both the benthic photographs and the coral health survey data.

Coral Reef Fish Abundance and Biomass

While slowly deploying the parallel 25-m transect lines, the surveyor identified to species and sized into 5-cm bins (*i.e.*, 0-5 cm, >5-10 cm, >10-15 cm, etc.) all fish within or passing through a 5-m wide belt along the transect. Each transect took between 10 and 15 minutes to complete. Individual fish biomass (=wet weight) was calculated using the mean length of the size bin and size-to-weight conversion parameters from FishBase (Froese and Pauly 2010), the USGS Hawaiʻi Cooperative Fishery Research Unit (HCFRU), and NOAA's Coral Reef Ecosystems Program. All fish surveys were conducted by trained and calibrated divers to reduce surveyor variability.

References

Beijbom, O., P. J. Edmunds, C. Roelfsema, J. Smith, D. I. Kline, B. Neal, M. J. Dunlap, V. Moriarty, T.-Y. Fan, C.-J. Tan, S. Chan, T. Treibitz, A. Gamst, B. G. Mitchell and D. Kriegman. 2015. Towards automated annotation of benthic survey images: variability of human experts and operational modes of automation. *PLOS One* 10(7): e0130312.

Froese, R. and D. Pauly. 2011. *FishBase.* World Wide Web electronic publication. www.fishbase.org, version (06/2011).

McCormick, M. 1994. Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. *Mar. Ecol. Prog. Ser.* 112: 87-96.