Evaluating Recovery of West Hawai‘i Reefs Eight Years Post-bleaching

Photos by TNC

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by

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Cover Photos (clockwise from upper left): a diver collects data on fish, a mixed school of surgeonfish swarm across a shallow reef site, finger and lobe corals at a deep reef site, and yellow tangs.

1.0 Executive Summary

In the fall of 2015, The Nature Conservancy (TNC) with its partners assessed the relative resilience potential of 20 reef locations along the west coast of Hawai‘i Island (West Hawai‘i), focusing on the reefs in the NOAA Habitat Focus Area in the districts of South Kohala and North Kona. At each location, 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 Hawai‘i was undergoing a mass coral bleaching event that affected nearly all coral species and extended to sites at least as deep as 15 m. The 2015 mass bleaching event was unprecedented in the Main Hawaiian Islands, and TNC conducted follow-up surveys in 2016, 2017, and 2019 to track reef response. The 2015 event resulted in considerable coral mortality, and although early signs of recovery were detected, by 2019 coral cover had not changed significantly and remained significantly lower than in 2015. In 2023, TNC and its partners returned to the same reef locations and repeated the benthic and fish surveys to assess the condition of the West Hawai‘i reef eight years after the 2015 mass bleaching event.

Thirteen coral species were identified during the 2023 surveys, with *Porites lobata* (lobe coral) and *P. compressa* (finger coral) accounting for almost 91% of all coral observations. Coral cover increased in 2023 (22.3 ± 3.4%) compared to 2019 (19.6 ± 1.6%) and 2017 (18.5 ± 1.4%), and for the first time since the bleaching event, did not significantly differ from pre-bleaching levels. The coral community as a whole followed a recovery trajectory that has seen coral and CAA, collectively known as reef-builders, increase in cover, while non-reefbuilder groups such as turf and abiotic substratum have decreased. Recovery of the benthic assemblage has shown a distinct spatial and depth pattern, with shallow reef sites and sites towards the middle of the survey area showing more recovery than deep reef sites and sites toward the northern and southern ends of the survey area. Reefs in shallow water were more severely affected by the mass bleaching event but have also experienced a more pronounced recovery.

A total of 122 species of reef fish in 28 families were observed in 2023. As in previous survey years, 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 across the survey area, whereas apex predators, such as jacks and barracuda, were rarely observed. Total fish biomass was 43.5 ± 7.7 g/m^2, down from 2019 (60.8 ± 12.7 g/m^2). However, it is unclear if this decline is the product of the high annual variability typical of reef fish populations or a "real" decline.

Using the timeseries data available for the 20 locations, resistance, recovery and net change effects were estimated. The resistance effect measured the change in coral cover following the mass bleaching event (change from 2015-2016). The recovery effect measured the change in coral cover in the eight years following the bleaching event (2016-2023), and the net change effect measured the difference in coral cover pre-bleaching and in 2023 (2015-2023). Only 39% and 35% of the survey sites showed resistance to the bleaching event and recovery, respectively, and only 32% of the sites were considered to be resilient, that is, they showed both resistance and recovery. The ability for a site to recover after being degraded proved more important than resisting the bleaching event when determining if a site had recovered to pre-bleaching levels, *i.e.*, the net change effect was zero or positive. The ability of a site to resist a bleaching event and to recover from the effects of such an event were not correlated, suggesting that different factors were influencing the two processes.

Land-based stressors such as sediment runoff, nutrient enrichment, and coastal development affect coral life history dynamics and ecosystems processes, and likely play a prominent role in coral reef community composition and condition. Using a large West Hawai‘i dataset compiled by Gove *et al.* (2023), we examined the relationship between land-based stressors, biophysical drivers such as wave exposure, and herbivore biomass on resistance, recovery and resilience. Land-based stressors showed no correlation with resistance, recovery and resilience. However, biophysical drivers and herbivore abundance at the time of the mass bleaching event were correlated with the net change effect. Sites with higher herbivore biomass in 2015 were more likely to have similar coral cover in 2023 as in 2015, but the relationship, while statistically significant, was weak.

These findings suggest the ability of West Hawai‘i reefs to weather temperature-related disruptions would benefit most from actions that improve reef recovery. This is especially true for reefs existing in less-than-ideal coral habitat, such as at depth in West Hawai‘i, where the potential for recovery is lower than in more favorable areas (*i.e.*, shallow reefs). While increased herbivore biomass and reduced land-based stressors have been shown previously to be associated with positive coral cover trajectories, actions that benefit herbivores, especially scrapers, would likely increase the recovery potential of West Hawai‘i reefs following a stressor event. These findings also highlight the increasing urgency for meaningful climate action as the frequency of mass bleaching events increases and the time interval available for reef recovery decreases. This study found little measurable reef recovery had occurred four years post-bleaching, and even eight years post-bleaching, reefs in West Hawai‘i have not returned to their pre-bleaching condition. Severe bleaching events occurring every few years would increase the likelihood of a gradual yet continuous degradation of West Hawai‘i’s coral reefs.

2.0 Introduction

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). It 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 encompasses two key components; 1) *resistance*, which is the ability of a reef to resist or survive a disturbance, and 2) *recovery*, which is the ability of a reef to return to its original condition following a disturbance (West and Salm 2003).

The west coast of Hawai'i Island (hereafter West Hawai'i) has one of the state's longest contiguous coral reef systems, which serves as habitat for culturally- and economically-significant species, mitigates wave and storm impacts, and provides recreational and other economic benefits (Cesar and van Beukering 2004).

In 2015, reefs globally experienced widespread severe coral bleaching (Eakin *et al.* 2022), including reefs on West Hawai'i (Kramer *et al.* 2016, Maynard *et al.* 2016). During this period, sea temperatures were elevated above the bleaching threshold (Degree Heating Weeks = 4 °C-weeks) for two months (NOAA CRW 2016), a level of thermal stress unprecedented in Hawai'i. 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 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. While encouraging signs of recovery were noted in 2017 (Minton *et al.* 2018a, Minton *et al.* 2018b), coral cover did not change significantly between 2016 and 2019 and remained significantly lower than that observed pre-bleaching in 2015 (Minton *et al.* 2020). Coral recruitment also appeared to decline, raising concerns about the long-term ability of these reef locations to recover from the 2015 bleaching and future stress events. The underlying cause(s) of this lack of reef recovery are likely associated with numerous factors, including stress from land-based sources such as sediment runoff and pollution.

In a study of the effects of integrated land-sea management on the condition of West Hawai'i reefs, Gove *et al.* (2023) found positive coral cover trajectories prior to the 2015 bleaching event on reefs were associated with increased herbivorous fish populations and reduced land-based stressors. These reefs also experienced lower coral mortality following the severe heat stress event in 2015 compared to reefs with reduced fish populations and enhanced land-based impacts. They concluded that both sea- and land-based management were necessary to increase the resistance of West Hawai'i reefs to large-scale stressor events. Recovery of reefs four years post-bleaching was not uniform or straightforward, but Gove *et al.* (2023) noted that decreased

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

wastewater pollution and increased herbivore-scraper biomass were the most important predictors of reef-builder (*i.e.*, corals and crustose coralline algae [CCA]) cover.

Reducing the degradation and improving the resilience of marine ecosystems is a goal within many management plans across Hawaiʻi and is regularly mentioned as important by stakeholders. Resilience-based management would be valuable in Hawaiʻi 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.* 2006), causing a disruption to commercially- and culturally-important fisheries. Therefore, considerable benefit would be gained by understanding the underlying mechanisms and the effects of various stressors on reef resilience.

In 2023, TNC returned to the same 20 reef locations surveyed in 2015, 2016, 2017, and 2019 to again document the condition and recovery of West Hawaiʻi reefs. This report describes the results of the 2023 surveys and builds upon pre-existing information to assess the current condition and trajectory of these West Hawaiʻi reef locations. It also investigates the relationship of herbivores and land-based stressors on reef resistance, recovery, and resilience.

3.0 Methods

The survey methods employed from 2015-2019 were originally developed to collect data 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 future effects of climate change (Maynard *et al.* 2016, Minton *et al.* 2018a). These included benthic cover, coral disease prevalence, density of juvenile corals (coral colonies ≤5 cm in diameter), rugosity, and reef fish abundance and biomass. However, these data did not produce reliably predictive rankings (Minton *et al.* 2020), so the data collection was reduced in 2023 and focused on benthic cover, rugosity, and reef fish abundance and biomass. These methods have been described in detail previously (Maynard *et al.* 2016, Minton *et al.* 2018a), and are summarized below.

3.1 Locations and Sites

The NOAA ESD, NOAA Habitat Blueprint, and Sentinel Site Program have had an overlapping Focus Area in West Hawaiʻi. These programs 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 was supported by, the NOAA Hawaiian Islands Humpback Whale National Marine Sanctuary, and was a focus of the NOAA National Marine Fisheries West Hawaiʻi Integrated Ecosystems Assessment Project.

In 2015, twenty locations were selected in for the reef resilience assessment in consultation with DAR, primarily within the North Kona and South Kohala Districts of West Hawaiʻi (Figure 1). Eighteen locations were spaced approximately ~2.5 kilometers apart within the Focus Area using ArcGIS and are representative of the full range of the area's ecological and physical conditions. Two additional locations (Honokōhau and Keauhou) were selected south of the Focus Area as management priorities for DAR. 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.

In 2016, TNC installed stainless steel pins at the start and end of each transect to permanently mark them for the 2016 and future resurveys. Site photos, field notes, GPS coordinates, and compass bearings collected in 2015 were used to realign the transects in 2016. 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 locations to avoid interference with DAR's ongoing monitoring efforts. Because TNC 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, sites with an offset between the 2015 and 2016 transect start location >35 m were removed when conducting multi-year analyses that include 2015 survey data (Table 1). This reduced dataset included a total of 27 sites, of which all

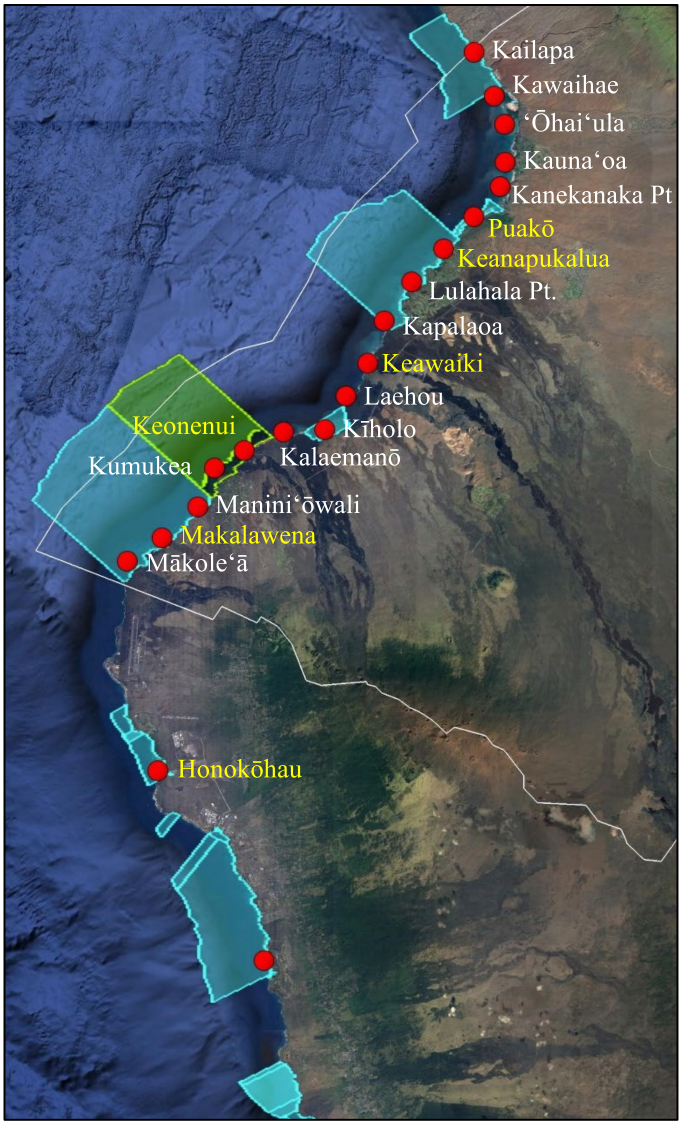

Figure 1. Map of survey locations, at each of which a shallow and deep site were surveyed. The white line is the boundary of the NOAA's West Hawaiʻi Focus Area. Blue polygons are State of Hawaiʻi Fishery Management Areas (FMAs) and Fishery Replenishment Areas (FRA). Both FMAs and FRAs have additional fishing restrictions compared to "open" areas. The green polygon is the Ka'ūpūlehu Marine Reserve. Two survey location (Kumukea and Keonenui) 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.

but three transects had offsets <25 m, which was below the spatial resolution of the original 2015 survey data. To distinguish between the datasets throughout this report, the *full dataset* comprised all survey sites and the *reduced dataset* comprised only sites with an offset <35 m.

3.2 Field Assessments

Survey work was completed between August 24-31, 2023. Previous surveys were conducted between late September and early November, but the early survey dates in 2023 were not expected to affect the benthic cover and fish abundance and biomass data.

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. The method for each survey type is summarized in Table 2, with more-detailed descriptions in Appendix B.

Table 1. 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 were included in the reduced dataset.

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
‘Ōhai‘ula	5.6	x	‘Ōhai‘ula	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	
Mākole‘ā	12.1	x	Mākole‘ā	2.6	x
Honokōhau	158.7		Honokōhau	124.5	
Keauhou	241.3		Keauhou	247.5	

3.3 Analysis

All fish and site metedata (*e.g.*, depth, rugosity, etc.) were entered into a custom Access database and checked for errors. Benthic data were compiled and verified in Excel spreadsheets prior to analysis. All databases and spreadsheets support safeguards to ensure high data quality, and they reside on a secure, cloud-storage platform that is backed up regularly to protect against data loss. Raw point data for the benthic photographs are maintained online in CoralNet.

3.3.1 Stressor Data

Data for land-based stressors (Table 3), including nutrients, impervious surfaces, onsite sewage disposal systems (OSDS), sediment, and wave energy (a natural stressor) were obtained from Gove *et al.* (2023). Stressors data were filtered using ArcGIS to select all data points within 100 m of each reef resilience transect. Filtered data were then averaged to produce a site-specific

Table 2. 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
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 to the nearest cm. The weight of each fish in grams was calculated using standard weight-length relationships and using coefficients sourced from FishBase, the USGS Hawaiʻi Cooperative Fishery Research Unit and NOAA's Coral Reef Ecosystem Program.

value for each land-based stressor (nutrients, impervious surfaces, onsite sewage disposal systems, and sediment) and wave energy. See Gove *et al.* (2023) for a description of the methods used to collect and compile the original stressor data.

For all datasets, the range of stressor values for the filtered data was narrower—sometimes considerably narrower—and the maximum values were considerably lower than in the original Gove *et al.* data. However, average values were always similar, suggesting the original data was heavily right skewed by a few very large values. While the TNC survey sites did not capture the upper range of the land-based stressors examined by Gove *et al.* (2023), they are representative of the typical range present on West Hawaiʻi reefs.

3.3.2 Statistical Analyses

Data for each site were obtained by averaging across the three transects. Variability in the starting conditions of the benthic assemblage at each site (*i.e.*, the initial coral cover and species composition observed in the 2015 surveys) made it challenging to make comparisons through time among the sites. Any potential change in benthic cover over time would be influenced by

Table 3. Description of the land-based stressor and wave action datasets obtained from Gove *et al.* (2023). See Gove *et al.* for the methods used to collect and compile these data.

Stressor	**Dataset**	**Description**
Nutrients	Nuts_2015 Nuts_2019	Nutrient input (kg/ha/yr) at 100 m resolution calculated as the combination of total nitrogen from OSDS and golf courses.
Impervious Surfaces	Imperv_2015 Imperv_2019	Total area of impervious surfaces (*e.g.*, paved roads, parking lots, sidewalks and roofs) within 10 km of the coastline at 100 m resolution for each year.
Onsite Sewage Disposal Systems	OSDS_Eff_2015 OSDS_Eff_2019	Wastewater effluent (L/ha/yr) and nitrogen input (kg/ha/yr) from onsite sewage disposal systems and injection wells in coastal waters at 100 m resolution.
Sediment	Sediment_2015 Sediment_2019	Long-term annual average sediment input (kg/ha) reaching the coast at 100 m resolution derived from the Integrated Valuation of Ecosystem Services and Tradeoffs sediment delivery model.
Wave energy	WPow975pct_2015 WPow975pct_2019	Wave power (kW/m), which combines wave height and period to provide a more representative metric of wave exposure than wave height alone.

the initial condition, *i.e.*, reefs that had higher initial coral cover had greater scope for loss or gain of coral. Therefore, absolute changes in benthic cover could not be used in most analyses to examine change over time. To account for this variability in starting condition, relative differences were used. Relative differences were calculated for each transect for time periods chosen to be representative of reef resistance (2015-2016), reef recovery (2016-2023), and the net change in reef condition (2015-2023). These were calculated for each transect as follows:

$$\text{Resistance} = \frac{(\text{Coral}_{2015} - \text{Coral}_{2016})}{(\text{Coral}_{2015})}$$

$$\text{Recovery} = \frac{(\text{Coral}_{2016} - \text{Coral}_{2023})}{(\text{Coral}_{2016})}$$

$$\text{Net change} = \frac{(\text{Coral}_{2015} - \text{Coral}_{2023})}{(\text{Coral}_{2015})}$$

The reduced dataset was used for the resistance and net change calculations and the full dataset was used for recovery calculation. A site's relative difference was calculated by averaging the relative difference calculated for each transect. To account for uncertainty arising from within site variability, the site's relative difference was divided by its standard deviation to obtain an "effect" value that was normalized as standard deviations away from zero, which represents no change in condition. Using guidance provided by Mastrandrea *et al.* (2010), these effect values could be aligned with basic probability statements, descriptors, and magnitudes of change (Table

Table 4. Basic probability statements, descriptors, and magnitudes of change for different effect sizes used in this report. Probability of Effect and Descriptors follow Mastrandrea *et al.* (2010).

Effect Size	Probability of Effect >0	Descriptor	Magnitude of change
>3	>99.7%	Virtually certain	Large positive
2 to 3	95 to 99.7%	Extremely likely	Medium positive
1 to 2	68 to 95%	Likely	Small positive
1 to -1	<68%	Less than likely	No change
-1 to -2	68 to 95%	Likely	Small negative
-2 to -3	95 to 99.7%	Extremely likely	Medium negative
<-3	>99.7%	Virtually certain	Large negative

4). For example, a net change effect of -2.1 at a site would be interpreted as that site being extremely likely to have experienced a medium-sized loss of coral cover between 2015 and 2023.

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 2015-2023 dataset were conducted using a mixed-model ANOVA with time and depth as fixed factors and site as a random factor to account for the non-independence of repeated measures at survey sites. Models were run for percent coral cover and biomass of all fish. Fish biomass was log+1 transformed to correct skewness and improve heteroscedasticity prior to analysis. 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. Change in benthic assemblage structure (coral, CCA, macroalgae, and other cover) was examined using PERMANOVA with survey year and depth as factors/covariates, with follow-up PERMANOVA pairwise comparisons. Given the natural variability of coral reef ecosystems, statistical significance was considered to be $p_{adj} \leq 0.05$ and "marginal" significance was $0.05 < p_{adj} \leq 0.10$. All ANOVA and PERMANOVA tables are included in Appendix C.

Non-metric multidimensional scaling (nMDS) was used to visualize the benthic assemblage and its change over time. nMDS was conducted on the percent cover of benthic groups (coral, CCA, macroalgae, and other) for all years using the reduced dataset. All sites were plotted using the first two components. To aid in visualizing recovery trajectories through time, centroids were calculated as the mean of all sites for each year and depth for each nMDS component and plotted onto the same figure.

The effect of land-based stressors on reef condition and resilience were examined using a Principal Component Analysis (PCA) of the data obtained from Gove *et al.* (2023) and herbivore and herbivore-scraper biomass obtained as part of TNC field surveys in 2015 or 2023 (see Section 3.2). Separate PCAs were conducted on all stressor and herbivore data from 2015 and 2019-2023. Eigenvector loadings were scaled proportionally to the eigenvalues to account for scale difference among the data inputs. Sites were visualized by plotting PCA1 against PCA2 for each analysis. The relationships between the resistance effect and the net change effects were examined by correlating the effect with PCA1 and PCA2 eigenvectors for the 2015 and 2019-2023 data, respectively.

All statistical analyses were conducted in R version 4.2.1 (2022-06-23). Final data were exported to Microsoft Excel for graphing and figure generation. The time series analyses were conducted using the 'lme4' and 'lsmeans' packages. All multivariate analyses were conducted using the "vegan" package, with follow-up PERMANOVA pairwise comparisons made using the "pairwise.adonis()" function developed by Pedro Martinez Arbizu. Throughout this report, means are presented as the average ± the standard error of the mean (SEM) unless otherwise stated.

4.0 Results and Discussion

4.1 Reef Condition: Eight Years Post-bleaching

4.1.1 Benthic Assemblage in 2023

Turf algae was the most common benthic cover type within the West Hawai‘i survey area, averaging 49.5 ± 3.0% cover (Table 5). Turf cover was lower in 2023 than in 2019 (63.1 ± 1.5%) and 2017 (63.7 ± 1.3%). Mean coral cover across the survey area was 22.3 ± 3.4%, which was slightly higher than in 2019 (19.6 ± 1.6%) and 2017 (18.5 ± 1.4%), suggesting an upward trend in coral cover. Coral cover was significantly higher at shallow than at deep sites, 26.5 ± 3.4% compared to 18.1 ± 3.2% (t-test; T_{36}=2.09, p=0.044). Thirteen 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 almost 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 7% of coral observations. Other coral species were rarely encountered (Table 5).

Table 5. Mean (±SEM) percent cover of major benthic groups/species in 2023.

	West Hawai‘i	**SHALLOW**	**DEEP**
Coral	22.3 ± 3.4	26.5 ± 3.4	18.1 ± 3.2
Porites lobata	16.7 ± 2.9	23.4 ± 3.1	10.0 ± 1.7
Porites compressa	3.5 ± 1.2	2.0 ± 1.0	5.0 ± 1.3
Porites monticulosa	1.4 ± 2.0	<0.1	2.8 ± 2.8
Montipora capitata	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.1
Porites rus	0.2 ± 0.2	0.3 ± 0.3	0
Porites evermanni/lutea	0.1 ± 0.3	0.3 ± 0.4	<0.1
Pavona varians	0.1 ± 0.1	0.1 ± 0.1	<0.1
Montipora patula	0.1 ± 0.1	0.1 ± 0.1	<0.1
Pavona duerdeni	0.1 ± 0.1	0.1 ± 0.1	<0.1
Pocillopora meandrina	0.1 ± 0.1	0.1 ± 0.1	<0.1
Psammocora stellata	<0.1	<0.1	<0.1
Fungia scutaria	<0.1	<0.1	0
Pocillopora damicornis	<0.1	<0.1	0
Turf	49.5 ± 3.0	50.8 ± 3.1	48.2 ± 3.0
Crustose Coralline Algae	15.5 ± 2.2	16.0 ± 1.9	15.1 ± 2.5
Other	0.5 ± 0.6	0.2 ± 0.2	0.7 ± 0.8
Macroalgae	<0.1	<0.1	<0.1
Cyanobacteria	<0.1	<0.1	<0.1
Abiotic	12.2 ± 2.4	6.5 ± 0.9	17.9 ± 2.7
Sand	7.7 ± 1.8	5.0 ± 0.9	10.4 ± 2.2
Rubble	4.5 ± 1.7	1.4 ± 0.5	7.5 ± 2.2
Recently Dead Coral	<0.1	<0.1	<0.1
Pavement	<0.1	<0.1	<0.1

4.1.2 Fish Assemblage in 2023

A total of 122 species of reef fish in 28 families were observed across the survey area in 2023. Total fish biomass was 43.5 ± 7.7 g/m^2 and varied from a low of 11.2 ± 2.0 g/m^2 (Kawaihae) to a high of 129.1. ± 52.8 g/m^2 (ʻŌhaiʻula). The high biomass at ʻŌhaiʻula was driven by an unusually high number of *Kyphosus* sp. (chubs) and *Monotaxis grandoculis* (bigeye emperors) observed at the location. Together these two species accounted for over 40% of the total fish biomass at ʻŌhaiʻula. Other than the 30 individuals observed at ʻŌhaiʻula, *Kyphosus* sp. were rarely observed during the 2023 surveys—only three other chubs were encountered at other locations combined. *M. grandoculis* were more frequently encountered at other locations, but generally only one to three individuals at a location, compared to the 32 individuals at ʻŌhaiʻula. These predators are often encountered singularly, but large adults are known to form aggregations of up to about 50 individuals. The two locations with the next highest total fish biomass were Makalawena and Honokohau, each with just over 76 g/m^2. In 2019, Manini'ōwali had the highest, and Kawaihae has had lowest total fish biomass in all surveys since 2016.

Acanthuridae (surgeonfishes) and Scaridae (parrotfishes) contributed the most to total fish biomass, 37%, and 13% of the total, respectively (Table 6). This was consistent with 2019 (Minton *et al.* 2020). These two families tend to be common on many Hawaiian reefs. Herbivores accounted for almost half the total fish biomass across the West Hawaiʻi survey area (Figure 2). Invertivores, such as bigeye emperors were 25% of the biomass. Apex predators, which include jacks, barracuda and jobfish, accounted for only 5% of the total fish biomass and were rarely observed, appearing on fewer than 7% of the transects. Apex predator biomass was considerably greater in shallow water, but this was primarily due to two whitetip sharks on the shallow transects at Makalawena. Without the two sharks, apex predator biomass would have been similar at both depths.

4.2 Reef Condition: Change Over Time

4.2.1 Benthic Assemblage Since 2015

Mean coral cover across the survey area significantly decreased between 2015 and 2016 and showed little recovery through 2019 (Figure 3). However, coral cover has increased since 2019 (ANOVA, $F_{4,190}$=3.78, p=0.006), and while still below 2015 levels, it was no longer significantly different from coral cover prior to the mass bleaching event. CCA has also increased since 2019 (Figure 3). Along with coral, CCA is an important reef-builder, and is a preferential settlement habitat for many corals (Heyward and Negri 1999, Jorissen *et al.* 2021). Since 2019, these reef-builders have increased at both deep and shallow sites, which is a positive sign that measurable recovery may finally be underway on West Hawaiʻi reefs. The increase in reef-builder cover has been offset by decreased cover of other, non-reef-building benthic components (Figure 3), a benthic group composed primarily turf and abiotic substratum[2].

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[2] Turf and abiotic substratum were measured separately starting in 2016; however, the 2015 surveys did not separate the two.

Table 6. Mean (±SEM) fish biomass by family (g/m^2) for West Hawai‘i and by depth in 2023. Biomass was not estimated for Muraenidae (eels) and Myliobatidae (rays). See Appendix B for more information.

Family	**West Hawai‘i**	**Shallow**	**Deep**
Acanthuridae (Surgeonfish)	16.0 ± 3.1	14.3 ± 1.8	17.7 ± 4
Scaridae (Parrotfish)	5.7 ± 1.5	7.5 ± 1.9	4.0 ± 0.8
Balistidae Triggerfish)	3.8 ± 0.9	5.2 ± 1.1	2.5 ± 0.6
Labridae (Wrasses)	3.2 ± 0.8	2.4 ± 0.3	4.1 ± 1.1
Holocentridae (Squirrelfish)	2.1 ± 1.6	0.9 ± 0.6	3.2 ± 2.2
Carcharhinidae Requiem sharks)	1.8 ± 2.7	3.7 ± 3.8	0
Lethrinidae (Emperors)	1.8 ± 1.9	2.7 ± 2.7	0.9 ± 0.5
Serranidae (Groupers)	1.7 ± 0.6	1.3 ± 0.5	2.0 ± 0.6
Mullidae (Goatfish)	1.6 ± 0.7	1.0 ± 0.4	2.1 ± 0.9
Pomacentridae (Damselfish)	1.6 ± 1.3	2.6 ± 1.8	0.5 ± 0.2
Kyphosidae (Chubs)	1.6 ± 2.2	0.1 ± 0.1	3.0 ± 3.1
Chaetodontidae (Butterflyfish)	1.4 ± 0.3	1.5 ± 0.3	1.4 ± 0.3
Carangidae (Jacks)	0.3 ± 0.2	0.2 ± 0.2	0.3 ± 0.2
Lutjanidae (Snappers)	0.2 ± 0.2	0.2 ± 0.1	0.3 ± 0.3
Aulostomidae (Trumpetfish)	0.1 ± 0.1	0.2 ± 0.1	0.1 ± 0.1
Cirrhitidae (Hawkfish)	0.1 ± 0.1	0.2 ± 0.1	0.1 ± 0.1
Fistulariidae (Cornetfish)	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.2
Zanclidae (Moorish Idol)	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Monacanthidae (Filefish)	0.1 ± 0.1	0	0.2 ± 0.2
Tetraodontidae (Pufferfish)	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Diodontidae (Porcupinefish)	0.1 ± 0.1	0.1 ± 0.1	0
Pomacanthidae (Angelfish)	<0.1	<0.1	0.1 ± 0.1
Synodontidae (Lizardfish)	<0.1	<0.1	<0.1
Ostraciidae (Boxfish)	<0.1	<0.1	<0.1
Blenniidae (Blennies)	<0.1	<0.1	<0.1
Apogonidae (Cardinalfishes)	<0.1	<0.1	<0.1
Muraenidae (Eels)	*	*	*
Myliobatidae (Rays)	*	*	*
TOTAL	**43.5 ± 7.7**	**44.4 ± 6.1**	**42.7 ± 9.3**

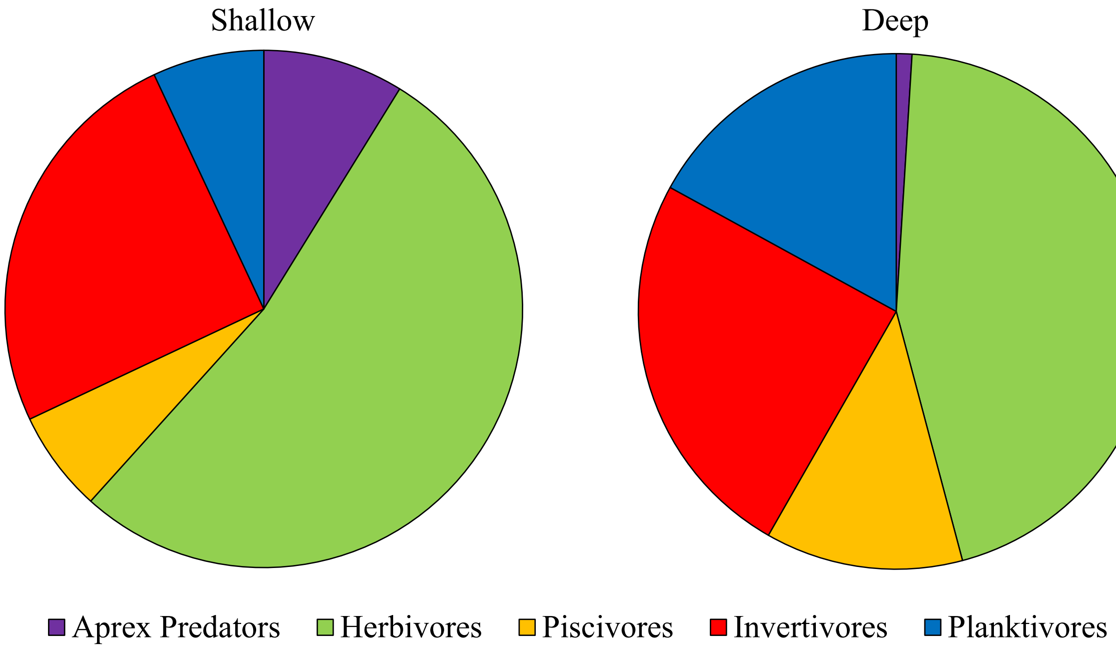

Figure 2. Trophic structure at shallow and deep sites across the West Hawai‘i survey area in 2023.

While our analysis did not detect a statistical difference in the recovery of the coral with depth (ANOVA, $F_{4,190}=0.46$, $p=0.764$), recovery appears to be happening at a slower rate at deep compared to shallow sites (Figure 3). At deep sites, the relative coral cover has increased only slightly between 2016 and 2023, 17% at deep compared to 31% at shallow sites. While shallow reef areas were more severely impacted by the mass bleaching event than deep reef areas, shallow sites are showing greater and faster recovery. Similar depth-dependent recovery has been observed elsewhere (Evans *et al.* 2020) and may be associated with more favorable conditions for coral growth in shallow compared to deep water.

The benthic assemblage as a whole has significantly changed since the 2015 mass bleaching event (PERMANOVA, $F_{1,136}=6.03$, $p=0.008$). Both deep and shallow sites have followed similar recovery trajectories (Figure 4). Coral losses from the 2015 mass coral bleaching event were initially offset by higher cover of CCA, macroalgae, and turf algae/abiotic substratum (Minton *et al.* 2018a). From 2016 to 2019, both deep and shallow reef areas recovered slightly, but non-reef-builder components became a more prominent component of the benthic assemble (Figure 5) and the recovery appeared to stagnate. However, by 2023, the benthic assemblage had shifted towards greater cover of reef-builders (Figure 4). The benthic assemblage in 2023 still differs significantly from that present in 2015, but it now appears to be on a trajectory favorable to coral recovery.

West Hawai‘i's reefs in general may be showing measurable recovery from the 2015 bleaching event, but that recovery has not been consistent across the survey area. Reefs near the middle of the survey area and especially in shallow water have coral cover in 2023 that is more similar to

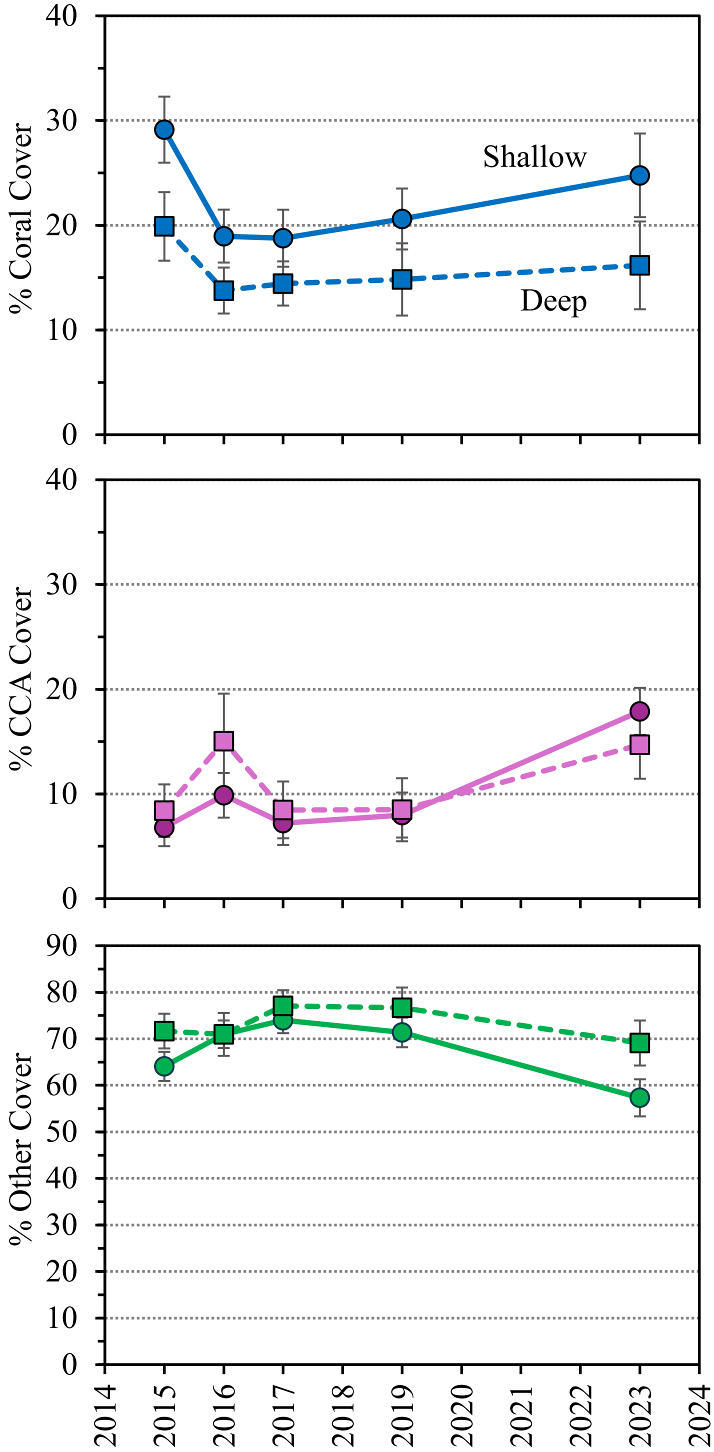

Figure 3. Mean (±SEM) percent cover of coral, CCA, and non-reef-builders (turf, abiotic, etc.) at shallow (circle, solid line) and deep (square, dashed line) sites between 2015 and 2023. Values were derived from the reduced dataset ($n_{shallow}$=13; n_{deep}=15), so annual points may vary slightly from values derived from the full dataset reported elsewhere in this and other reports.

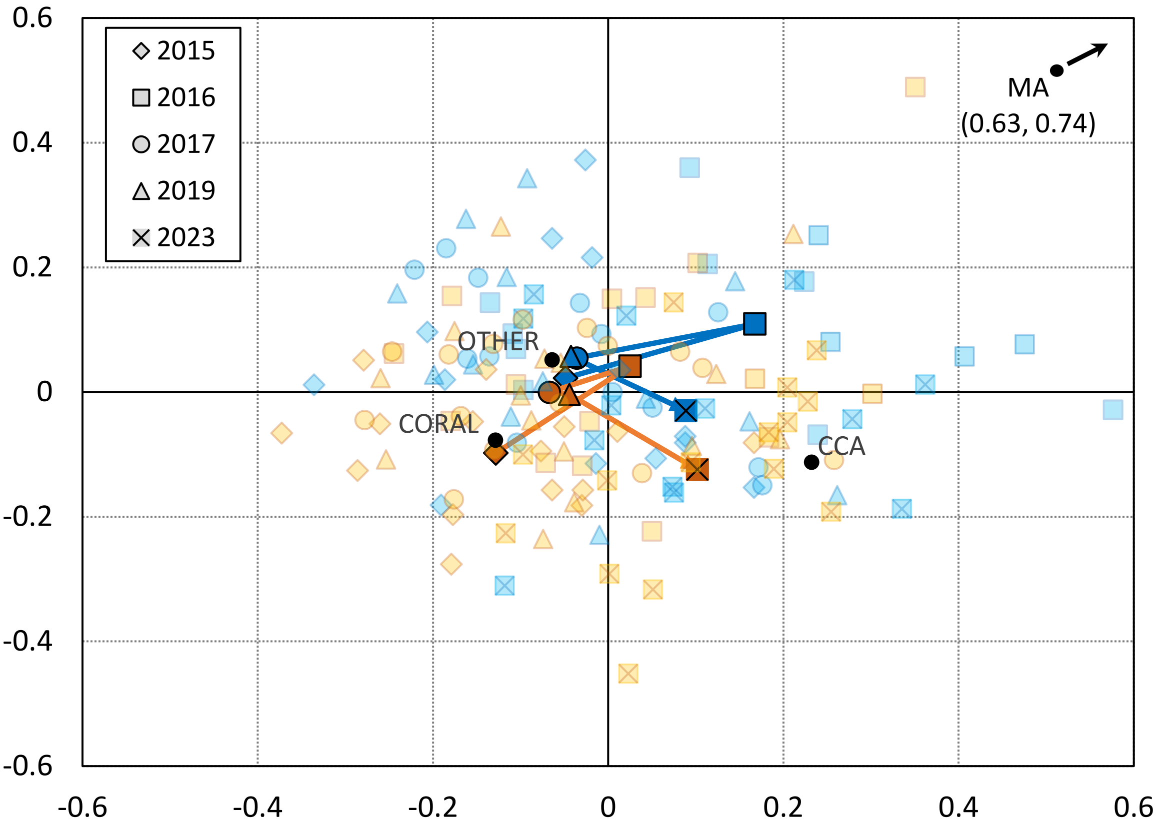

Figure 4. Change in the benthic assemblage from 2015 to 2023 at deep (blue) and shallow (orange) sites. Solid shapes and lines track the “average” deep and shallow reef assemblages on West Hawaiʻi, and transparent points are the raw site data. Points in the top half of the ordination graph are benthic assemblages best characterized as “non-reef-builder,” whereas those on the bottom half of the of the graph are assemblages best characterized as “reef-builder.” Both deep and shallow reef areas show similar recovery trajectories. CCA=Crustose Coralline Algae, MA=Macroalgae, OTHER=primarily turf and abiotic substratum.

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that which was present in 2015, prior to the mass coral bleaching event than sits on the northern and southern ends of the survey are an at deep sites (Figure 6). In general, these central reef areas experienced both lower coral loss from the bleaching event (Figure 7) and greater recovery (Figure 8) than reef areas to the north and south. Potential reasons for this will be explored in later sections of this report.

4.2.2 Fish Assemblage Since 2015

Total fish biomass has shown considerable temporal variability but was lower in 2016, 2017, 2019 and 2023 when compared to 2015 (Figure 9). In 2017, total fish biomass dipped to 35.4 ± 7.2 g/m^2, significantly lower than that observed in 2015 and 2016 (ANOVA, $F_{4,190}$=4.99, p<0.001), but it was unclear if this decline was the product of the high annual variability typical of reef fish populations or a "real" decline. Minton *et al.* (2018b) provided additional context to

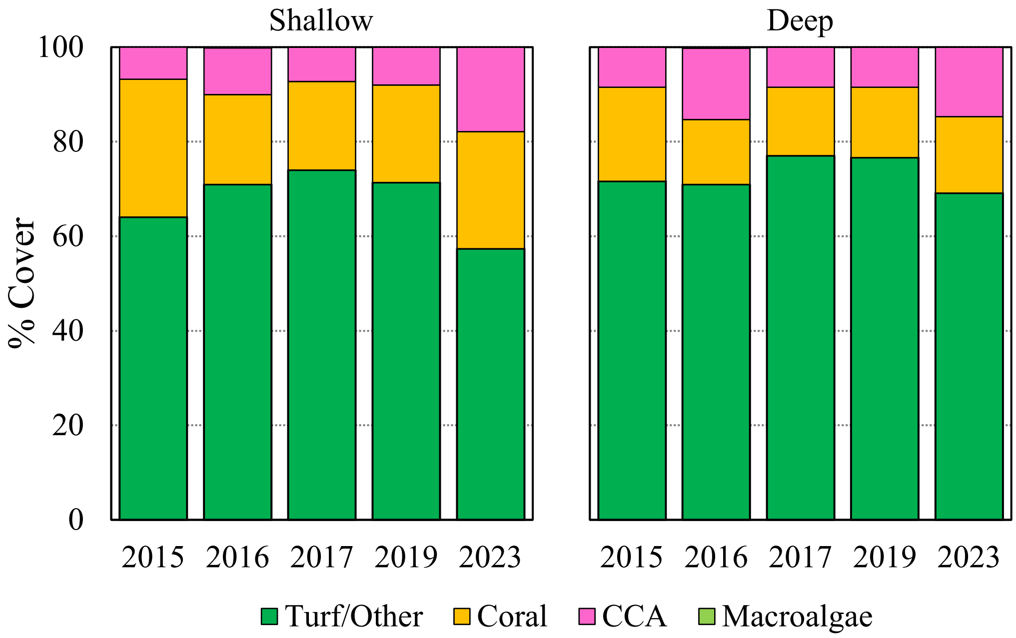

Figure 5. Mean percent cover by benthic group at shallow and deep sites along West Hawai‘i from 2015-2023. Values were derived from the reduced dataset ($n_{shallow}$=13; n_{deep}=15), so annual values may vary slightly from those derived from the full dataset reported elsewhere in this and other reports.

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interpret the lower total fish biomass observed in 2017 and concluded that while the trend appeared to be "real" it was likely the result of a "relaxation" from a spike in biomass associated with a large reef fish recruitment event that occurred in 2014. Since 2017, total fish biomass has fluctuated but has remained lower than that observed in 2015 and only slightly greater than that observed 2017 (Figure 9). Shallow and deep reef areas on West Hawai‘i reefs are responding similarly, which would be consistent with the conclusion of Minton *et al.* (2018b). However, high annual variability in the fish population makes it difficult to separate the effects of the 2014 recruitment event and any possible declines associated with the effects of the mass bleaching event. West Hawai‘i reefs appear to have settled into an equilibrium condition that has lower biomass of all fish and herbivores than was present in 2015, prior to the bleaching event, but also a year after the large reef fish recruitment event (Figure 9). Unfortunately, a directly comparable dataset is not available for the survey area prior to 2014. 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, Foo *et al.* 2021), so a regional trend should not be ruled out, but given the high temporal variability in the data, a longer timeseries would be needed to identify it.

4.3 Reef Resilience

Resilience is generally assumed encompasses two key components: resistance and recovery (West and Salm 2003). While several conceptual approaches to resilience exist (Lam *et al.* 2020), TNC as taken an approach to assess climate vulnerability using static or snapshot indicators because this approach has the potential to integrate well with existing field monitoring

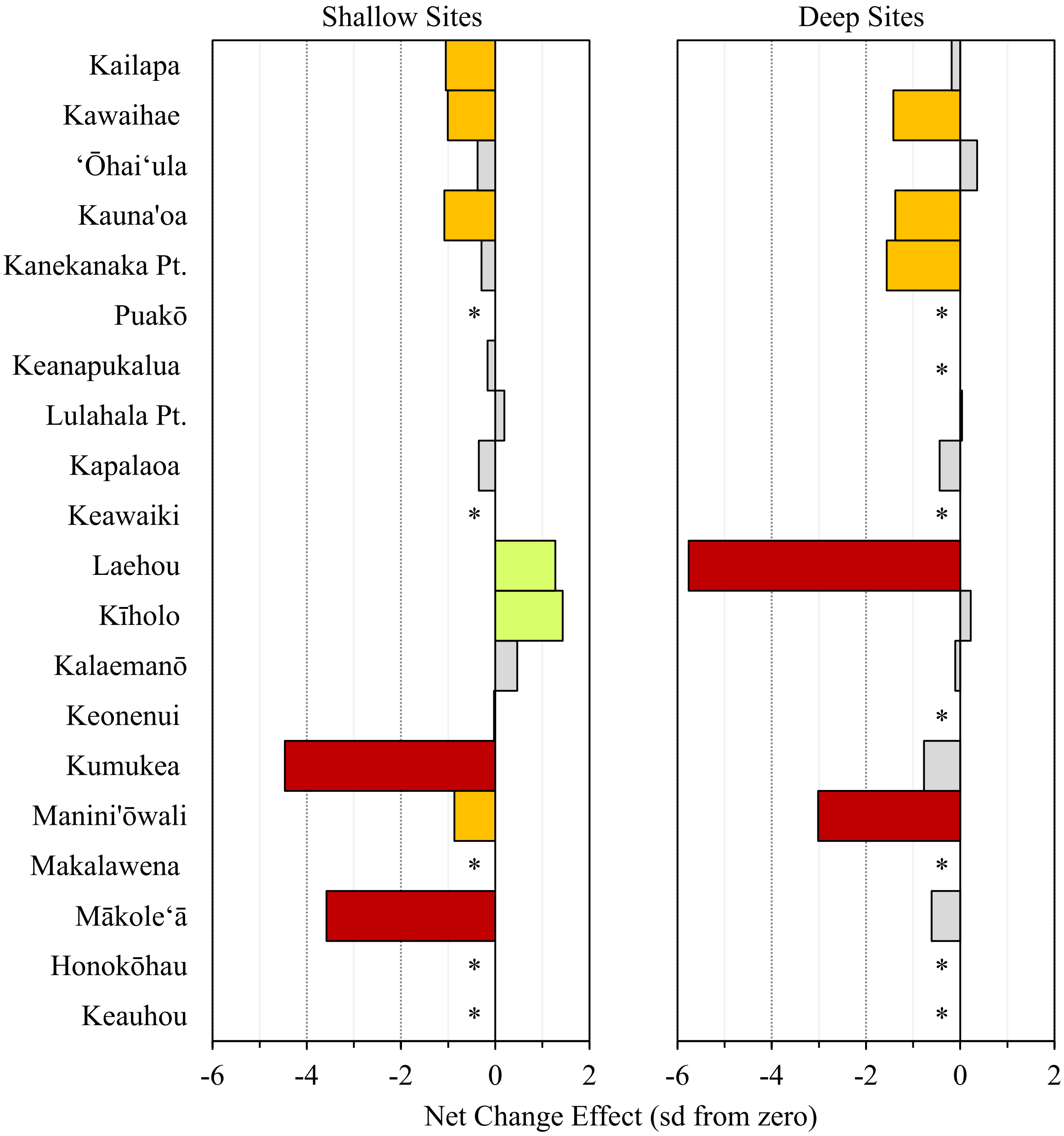

Figure 6. Net change effect for coral cover between 2015 and 2023 at shallow (left) and deep (right) sites on West Hawai‘i. Negative values (orange and red bars) represent locations that are likely to have less coral cover in 2023 than in 2015. Positive values (green bars) are locations likely to have more coral cover in 2023 than in 2015. Grey bars represent locations likely to have similar coral cover in 2023 and 2015. Sites are arranged from most northerly (top) to most southerly (bottom). Asterisks (*) indicate locations not included in the reduced dataset; see methods for more information on the reduced dataset.

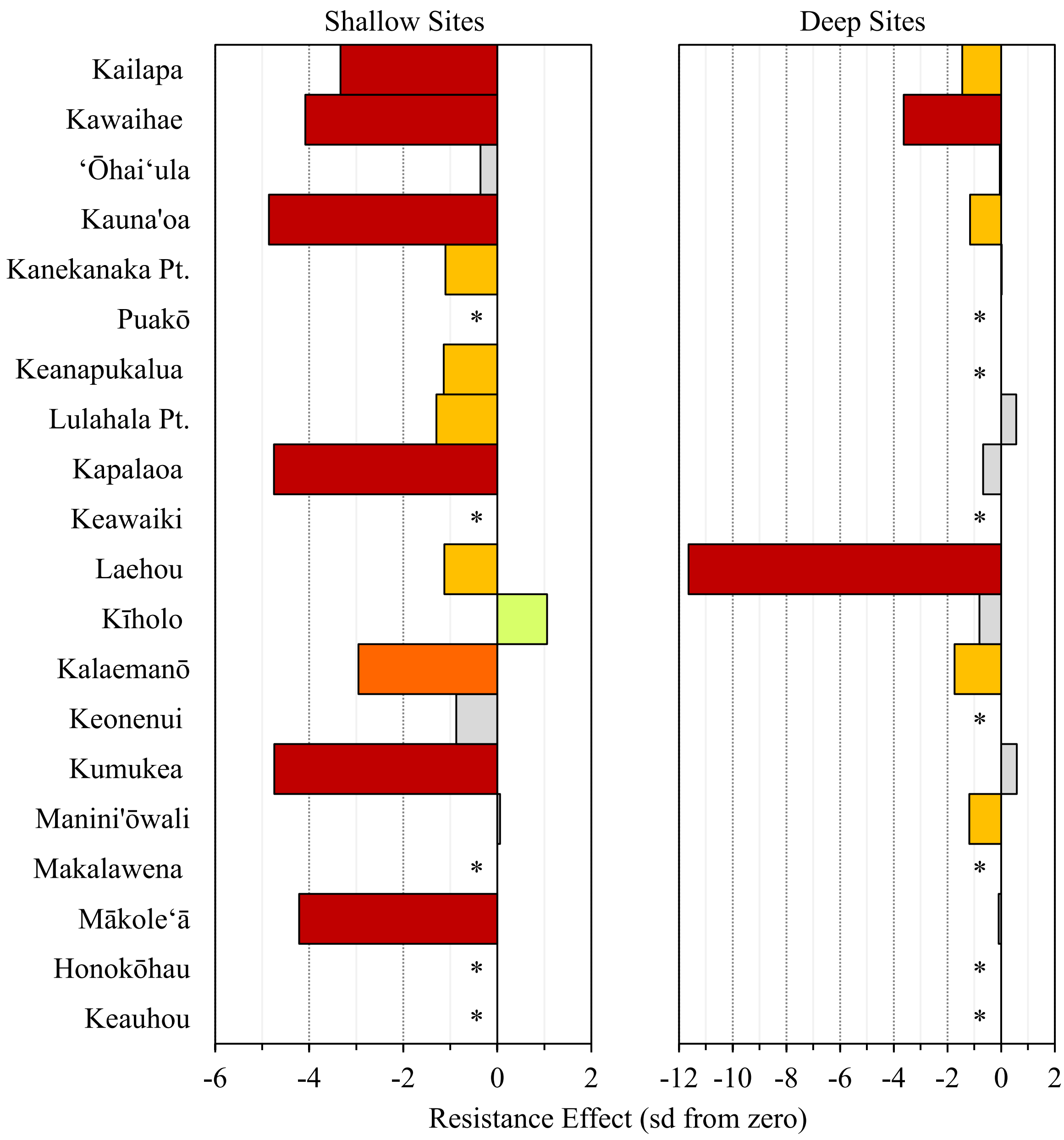

Figure 7. Resistance effect for coral cover between 2015 and 2016 at shallow (left) and deep (right) sites on West Hawai‘i. Negative values (orange and red bars) represent locations that are likely to have less coral cover in 2016 than in 2015. Positive values (green bars) are locations likely to have more coral cover in 2016 than in 2015. Grey bars represent locations likely to have similar coral cover in 2016 and 2015. Sites are arranged from most northerly (top) to most southerly (bottom). Asterisks (*) indicate locations not included in the reduced dataset; see methods for more information on the reduced dataset.

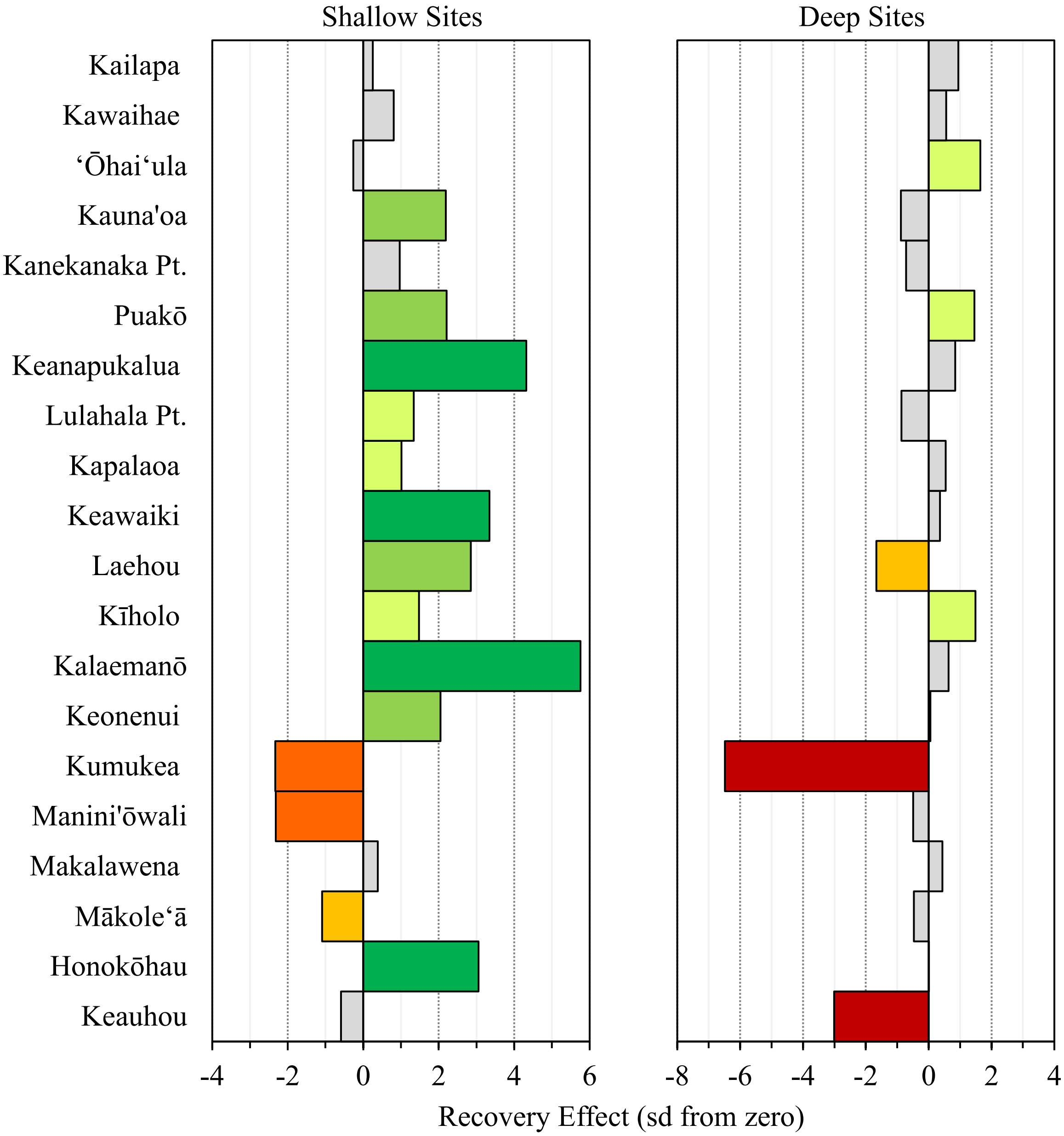

Figure 8. Recovery effect for coral cover between 2016 and 2023 at shallow (left) and deep (right) sites on West Hawai‘i. Negative values (orange and red bars) represent locations that are likely to have less coral cover in 2023 than in 2016. Positive values (green bars) are locations likely to have more coral cover in 2023 than in 2016. Grey bars represent locations likely to have similar coral cover in 2023 and 2016. Sites are arranged from most northerly (top) to most southerly (bottom).

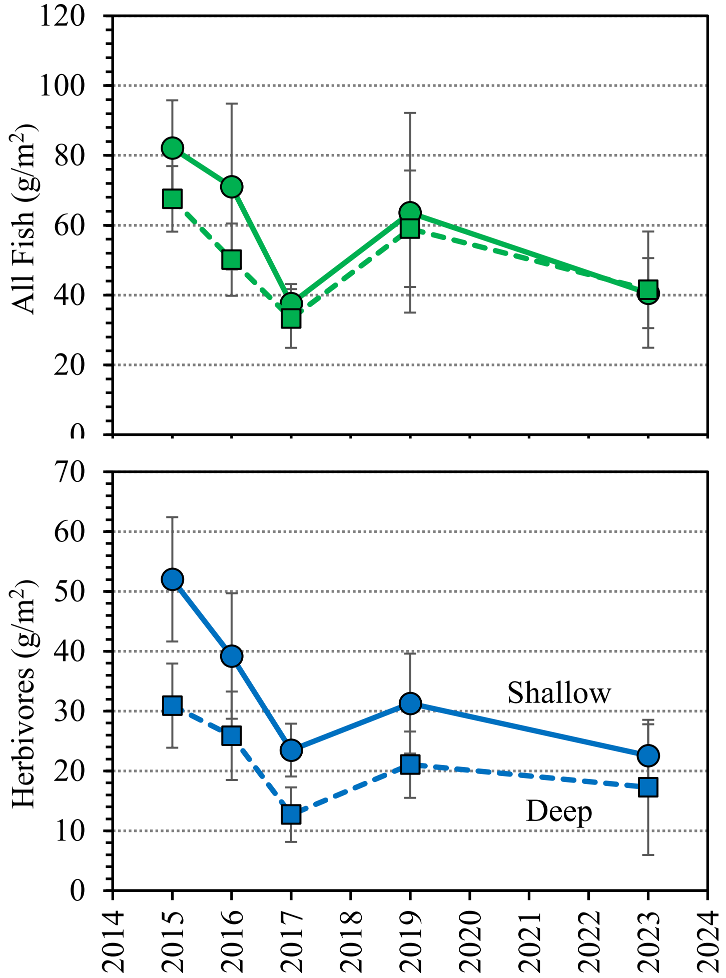

Figure 9. Mean (±SEM) total fish and herbivore biomass at shallow (circle, solid line) and deep (square, dashed line) sites between 2015 and 2023. Values were derived from the reduced dataset ($n_{shallow}$=13; n_{deep}=15), so annual points may vary slightly from values derived from the full dataset for a given year.

programs. In 2015, TNC developed rankings for the relative resilience potential for both deep and shallow sites at 20 locations in West Hawai‘i (Maynard *et al.* 2016). These rankings used primarily biological indicators to order sites by estimated resilience potential, from most resilient (rank 1) to least resilient (rank 20). The 2015 mass coral bleaching event (and to some extents a less severe 2019 event) provided a unique opportunity to assess the performance of these rankings. Overall, the reef resilience rankings proved to be poor predictors for both resistance and recovery (Minton *et al.* 2020), suggesting the suite of factors incorporated into the formulation of the resilience rankings were poor predictors in Hawai‘i, and that other factors may be influencing reef processes. Minton *et al.* (2020) suggested revisiting the resilience of the West Hawai‘i sites using an approach that encompassed both resistance and recovery, and to not necessarily combine them into a single unified resilience score or rank. Highlighting the variability in resistance and recovery may shed light on the inherent differences among reefs and may provide greater insight into the processes that are most important for ensuring a location's long-term persistence, especially when challenged by future climate-related events. Given the data now available, it is possible to directly identify locations/sites that showed positive resistance to and recovery from the 2015 mass bleaching event. Sites that show both positive resistance and recovery could be consider “resilient.”

Sites within the West Hawaiʻi survey area showed considerable variability in their resistance and recovery. Eleven of 28 sites (39%) showed either no change or a small increase in coral cover from 2015 to 2016 (grey or green bars in Figure 7), that is, these reef sites resisted the adverse effects of the 2015 mass bleaching event. These locations tended to be in the middle of the survey area and at deeper sites.

Since 2016, 14 of 40 sites (35%) have increased in coral cover, indicating they have shown some degree of recovery (green bars in Figure 8). These locations also tended to be in the middle of the survey area and were more frequently shallow sites. Twenty sites (50%) have shown no change in coral cover since 2016, with most of these being in deep water (grey bars in Figure 8).

Only four of 28 sites (14%) showed both resistance and recovery: ʻŌhaiʻula deep, Kīholo shallow, Kīholo deep, and Keonenui shallow (Table 7). An additional five sites (18%) showed resistance but a recovery that did not result in an increase or decrease in coral cover: ʻŌhaiʻula shallow, Kanekanaka Pt. deep, Lulahala Pt. deep, Kapalaoa deep, and Mākoleʻā deep. Given these sites showed no initial adverse effect, they did not "need" to recover and were also considered resilient based on their initial resistance to the 2015 mass bleaching event (Table 7).

Table 7. Summary of resilience by depth and location. A site was determined to have resilience if it showed: 1) resistance that resulted in no change (=) or a positive change (+) in coral cover <u>and</u> a positive recovery or 2) resistance that resulted in no change (=) <u>and</u> a recovery that showed no change (=). Sites that showed any negative change (-) were not considered resilient. Resilience could not be determined for 11 sites due to an inability to determine its resistance.

Location	**Shallow**		**Deep**	
Kailapa	Resistance: - Recovery: =	Not Resilient	Resistance: - Recovery: =	Not Resilient
Kawaihae	Resistance: - Recovery: =	Not Resilient	Resistance: - Recovery: =	Not Resilient
ʻŌhaiʻula	Resistance: = Recovery: =	Resilient	Resistance: = Recovery: +	Resilient
Kauna'oa	Resistance: - Recovery: +	Not Resilient	Resistance: - Recovery: =	Not Resilient
Kanekanaka Pt.	Resistance: - Recovery: +	Not Resilient	Resistance: = Recovery: =	Resilient
Puakō	Resistance: ? Recovery: +	?	Resistance: ? Recovery: +	?
Keanapukalua	Resistance: - Recovery: +	Not Resilient	Resistance: ? Recovery: =	?
Lulahala Pt.	Resistance: - Recovery: +	Not Resilient	Resistance: = Recovery: =	Resilient
Kapalaoa	Resistance: - Recovery: +	Not Resilient	Resistance: = Recovery: =	Resilient

Table 7 (continued).

Location	Shallow		Deep	
Keawaiki	Resistance: ? Recovery: +	?	Resistance: ? Recovery: =	?
Laehou	Resistance: - Recovery: +	Not Resilient	Resistance: - Recovery: -	Not Resilient
Kīholo	Resistance: + Recovery: +	Resilient	Resistance: = Recovery: +	Resilient
Kalaemanō	Resistance: - Recovery: +	Not Resilient	Resistance: - Recovery: =	Not Resilient
Keonenui	Resistance: = Recovery: +	Resilient	Resistance: ? Recovery: =	?
Kumukea	Resistance: - Recovery: -	Not Resilient	Resistance: = Recovery: -	Not Resilient
Manini'ōwali	Resistance: = Recovery: -	Not Resilient	Resistance: - Recovery: =	Not Resilient
Makalawena	Resistance: ? Recovery: =	?	Resistance: ? Recovery: =	?
Mākole‘ā	Resistance: - Recovery: -	Not Resilient	Resistance: = Recovery: =	Resilient
Honokōhau	Resistance: ? Recovery: +	?	Resistance: ? Recovery: =	?
Keauhou	Resistance: ? Recovery: =	?	Resistance: ? Recovery: -	Not Resilient

Not surprisingly, sites designated as resilient have fared better than sites designated as not resilient, with resilient sites showing larger average net gain effect than non-resilient ones (Table 8). However, sites in shallow water tended to fare better than sites in deep water, regardless of their resilience status. The ability of a reef to recover from the mass bleaching event was the key factor determining whether a reef had similar coral cover in 2015 and 2023. Reefs with a low recovery effect usually had lower coral cover in 2023 compared to 2015 (Figure 10), regardless of the magnitude of their resistance effect. On average, if a reef experienced no recovery (recover effect = 0), it was likely to experience a small but negative net change (net change effect = -1.02) in coral cover eight years post-bleaching. In contrast, reefs with a negative resistance effect could still return to, and at times even exceed, their 2015 coral cover because these sites could still benefit from a large recovery. On average, reef areas that experienced no resistance effect (resistance effect = 0), showed essentially no net change eight years post-bleaching (net change = -0.01). The ability of a site to resist a bleaching event and to recover from the effects of such an event were not correlated (Correlation; r=004; p=0.979). This lack of correlation between a site's resistance and recovery suggests that different factors are influencing the two processes.

Table 8. Mean (±SEM) resistance (2015 to 2016), recovery (2016 to 2023), and net change (2015 to 2023) effect for coral cover at resilient and non-resilient shallow and deep sites on West Hawaiʻi. Positive effects indicate an increase in coral cover. Interpretation of effect values can be found in Section 3.3.

	Resistance	**Recovery**	**Net Change**
Shallow Sites			
Resilient	0.67 ± 0.57	1.02 ± 0.74	0.34 ± 0.32
Non-resilient	-0.91 ± 0.53	-2.97 ± 1.33	-0.91 ± 0.49
Deep Sites			
Resilient	-0.39 ± 0.27	0.33 ± 0.07	-0.33 ± 0.32
Non-resilient	-1.98 ± 0.95	-7.38 ± 2.29	-1.81 ± 0.82

These findings suggest the ability of West Hawaiʻi reefs to weather temperature-related disruptions would benefit most from actions that improve reef recovery. This is especially true for reefs existing in less-than-ideal coral habitat, such as at depth in West Hawaiʻi, where the potential for recovery is lower than in more favorable areas (*i.e.*, shallow reefs). It also increases the urgency for undertaking meaningful climate action; as the frequency of mass bleaching events increases, the time interval available for reef recovery decreases. This study found little measurable reef recovery had occurred four years post-bleaching, and even eight years post-bleaching, reefs in West Hawaiʻi have not returned to their pre-bleaching condition. Severe bleaching events occurring every few years would increase the likelihood of a gradual yet continuous degradation of West Hawaiʻi's coral reefs (Babcock *et al.* 2021, Brown *et al.* 2023).

4.3 Land-based Stressors and Reef Resilience

Minton *et al.* (2018a) explored the relationship of environmental stressors 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.

Using a larger West Hawaiʻi dataset, Gove *et al.* (2023) found West Hawaiʻi reefs with increased herbivorous fish populations and reduced land-based impacts, especially wastewater pollution and urban runoff, experienced a modest reduction in bleaching-related coral loss when compared to reefs with reduced fish populations and enhanced land-based impacts. Land-based stressors such as sediment runoff, nutrient enrichment, and coastal development affect coral life history dynamics and ecosystems processes. Variability in these anthropogenic and other land-based stressors, as well as variation in biophysical drivers such as wave exposure across the West Hawaiʻi survey area, likely play a important role in coral reef community composition and condition.

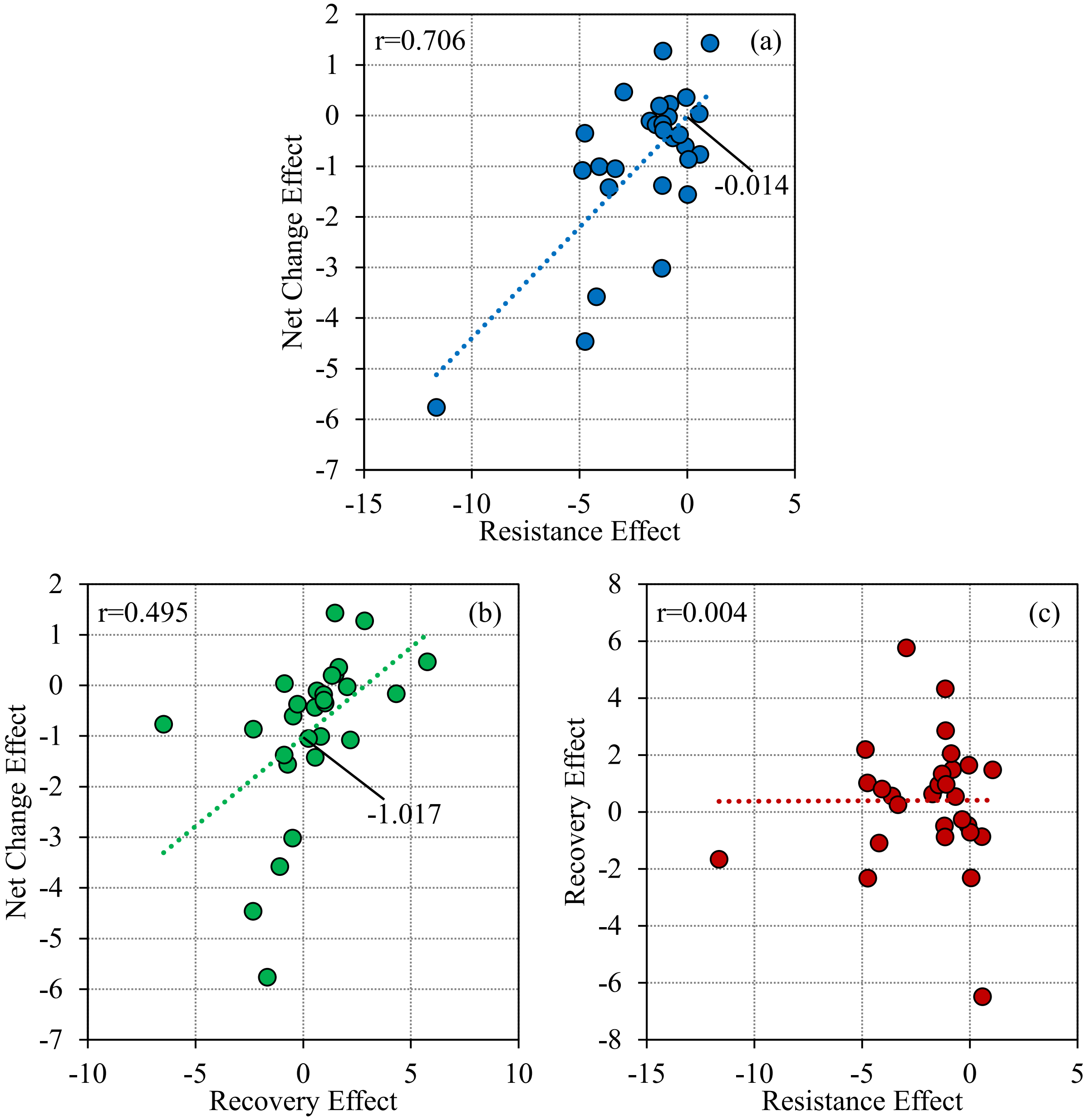

Figure 10. Relationship of the (a) resistance and net change effects, (b) recovery and net change effects, and (c) resistance and recovery effects.

The 2015 and 2019/23 PCAs produced similar results, which given the non-independence of the two datasets is not surprising—the stressors have changed little over the intervening years between the two datasets. The first two eigenvectors explained 55% and 58% of the variability in 2015 and 2019/23, respectively. In both analyses, PCA1 had high positive loadings for anthropogenic, land-based sources of stress (Table 9). This eigenvector captured the influence of the impervious surfaces, nutrient enrichment, and wastewater, and higher land-based stressors would result in large positive PCA1 values. The interpretation of PCA2 differed slightly between the two analyses but had considerable overlap. Ocean-based factors—wave power and herbivore

Table 9. The first two eigenvectors from the PCA for 2015 and 2019/23. Component loadings are scaled proportional to eigenvalues.

Stressors	2015		2019/23	
Stressors	**PC1**	**PC2**	**PC1**	**PC2**
Impervious Surface	1.20	-0.07	1.14	-0.20
OSDS	1.15	-0.05	1.14	-0.38
Nutrients	1.18	0.43	1.18	0.14
Sediment	0.27	-0.54	-0.19	-1.15
Wave Energy	-0.68	0.96	-0.63	1.03
Total Herbivores	0.67	0.88	0.60	0.61
Herbivores-scrapers	-0.15	1.09	0.61	0.89
Eigenvalue	2.34	1.53	2.33	1.71
Prop. Explained	0.33	0.22	0.33	0.24
Cum. Prop.	0.33	0.55	0.33	0.58

biomass—had moderate to high loadings in both 2015 and 2019/23. In 2015, other loadings were relatively small, but in 2019/20, PCA2 had a large negative loading for sediment. For both analyses, this eigenvector captures primarily the positive role of ocean-based factors among the survey sites. Sites with ample mixing and high herbivore biomass and low sediment would have larger positive PCA2 values in both analyses.

When PCA1 vs PCA2 were plotted (Figure 10), locations were distributed in the ordination space as expected. For example, nutrient and OSDS (*i.e.*, septic systems and cesspools) issues at Puakō are well-documented, and in both analyses, shallow and deep sites at Puakō had high PCA1 loadings. Similarly, both shallow and deep sites at Kawaihae and the deep site at Kailapa had large negative loadings for PCA2. Both locations have upland erosion challenges, which contribute to sediment issues on the nearshore reef, and Kawaihae has consistently had low herbivore biomass.

None of the three effects were significantly correlated with PCA1 from either the 2015 or the 2019/23 datasets (Table 10). Anthropogenic, land-based stressors did not explain a significant amount of the variability in resistance, recovery or net change over time within the West Hawai‘i survey area. PCA2 for the 2015 data was significantly correlated with the net change effect, however, it explained only 13.5% of the variability. Ocean based factors, especially herbivore biomass, have been shown to have a positive effect on reef condition (Williams *et al.* 2019, Donovan *et al.* 2023) and may beneficially affect reef recovery following climate stress events (Raj *et al.* 2021, Gove *et al.* 2023). While not statistically significant, the correlation between the recovery effect and PCA2 for the 2015 dataset was the second largest.

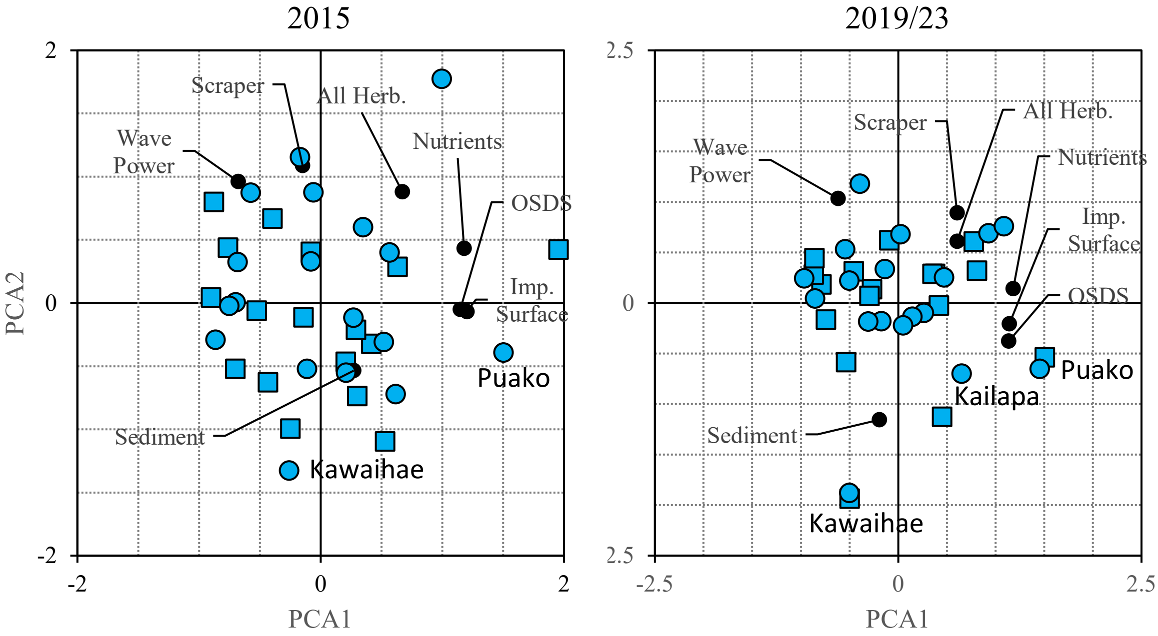

Figure 11. Ordination plots for deep (square) and shallow (circle) survey locations in West Hawai‘i reefs for 2015 and 2019/23. Data are from Gove *et al.* (2023). See section 3.3 for more details.

Table 10. Correlation (r) among resistance, recovery and net change effects and the first two principal components for from the 2015 and 2019/23 PCA. Asterisk (*) indicates the correlation coefficient was significant at p=0.05.

	2015		**2019/23**	
Effect	**PC1-2015**	**PC2-2015**	**PC1-2019**	**PC2-2019**
Resistance (2015-2016)	0.134	-0.094	-	-
Recovery (2016-2023)	-0.073	-0.198	-0.068	-0.132
Net Change (2015-2023)	-0.043	-0.368*	-0.022	-0.083

5.0 Conclusions

While a focus of considerable work, understanding resilience in marine ecosystems is still in its nascent phase. 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, yet the science of resilience remains primarily theoretical. The complexities of ecological communities arise through their functional and genetic diversity and the myriad of interactions that occur across multiple spatial and temporal scales and among biological, physical and chemical components of the ecosystem. Indeed, recent studies looking at the recovery dynamics of coral reefs around the world have found the resilience drivers most important for recovery can vary considerably between regions (Graham *et al.* 2015).

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) would allow for more effective use of limited resources through the better targeting of the types and locations of management actions. However, our ability to predict reef resilience prior to a stressor event has been unsuccessful to date in West Hawaiʻi. Using an eight-year dataset around the 2015 mass bleaching event in West Hawaiʻi, we identified recovery (as opposed to resistance) as the key process that increased the likelihood of a reef area returning to pre-bleaching levels of coral cover.

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 following the bleaching event, these reefs showed little recovery, but eight years post-bleaching, average coral cover across the survey area did not significantly differ from pre-bleaching levels. This result was spatially variable, with reefs at the northern and southern edges of the survey, showing linger negative effects, which was likely due to an inability of the coral within these reef areas to recover from initial losses.

Management actions that improve coral recovery following a mass bleaching event are likely to produce the largest benefit to reef resilience. Intuitively, this would include reducing the influence of anthropogenic, land-based stressors. However, we were unable to establish a clear relationship between several land-based stressors and recovery effects. Additional research is needed to identify how best to enhance reef recovery rates, especially as recovery times are anticipated to shorten as climate-related stress events increase in frequency in Hawaiʻi.

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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- Mākole‘ā Netting Restricted Area
17	Makalawena	S: (19.79692, -156.0268) D: (19.79738, -156.02708)	Kikaua Pt- Mākole‘ā Netting Restricted Area; DAR Long-term Monitoring Site
18	Mākole‘ā	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

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 all fish within or passing through a 5-m wide belt along the transect. In 2015, 2016, and 2017, fish were sized into 5-cm bins (*i.e.*, 0-5 cm, >5-10 cm, >10-15 cm, etc.), but in subsequent survey years, fish were sized to the nearest centimeter. 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. The biomass of Muraenidae (Eels), Myliobatidae (manta rays) and *Decapterus macarellus* (mackerel scad or ʻōpelu) was not included the estimation of total fish biomass. Eels could not be accurate sized and manta rays and mackeral scad are transient fish seldom observed on transects; however, when present, they heavily skew the transect estimates due to their large size or their presence in very large schools.

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Appendix C.

Table C.1. Repeated measures ANOVA table for coral cover by year and depth. Year and depth were fixed factors and site was random. Significance was assessed using Type II Wald F tests with Kenward-Roger degrees if freedom (residual df=190). P-values for multiple comparisons were adjusted using the Tukey method. Multiple comparisons between years were averaged over depth.

	df	Sum Sq	Mean Sq	F-value	p
Year	4	806.86	201.71	3.78	0.006
Depth	1	711.67	711.67	13.35	<0.001
Year*Depth	4	98.30	24.57	0.46	0.764

Pair	Diff	T ratio	P-adj
2015-2016	7.28	3.26	0.0115
2015-2017	7.02	3.14	0.0167
2015-2019	5.93	2.65	0.0654
2015-2023	3.22	1.44	0.6029
2016-2017	-0.27	-0.12	1.0000
2016-2019	-1.36	-0.61	0.9740
2016-2023	-4.06	-1.82	0.3667
2017-2019	-1.09	-0.49	0.9885
2017-2023	-3.80	-1.70	0.4375
2019-2023	-2.72	-1.21	0.7449

Table C.2. PERMANOVA table for benthic cover by group (coral, CCA, macroalgae, and other) by year and depth.

	df	Sum Sq	Mean Sq	F-value	p
Year	1	0.114	0.040	6.03	0.008
Depth	1	0.167	0.058	8.80	0.002
Year*Depth	1	0.034	0.012	1.82	0.154
Residual	136	2.574	0.891		

Pair	F	R^2	P-adj
2015-2016	5.05	0.086	0.09
2015-2017	7.24	0.118	0.03
2015-2019	4.36	0.075	0.21
2015-2023	5.39	0.091	0.12
2016-2017	2.05	0.037	1.00
2016-2019	1.26	0.023	1.00
2016-2023	3.77	0.065	0.50
2017-2019	0.20	0.004	1.00
2017-2023	10.98	0.169	0.02
2019-2023	7.79	0.126	0.05

Table C.3. Repeated measures ANOVA table for total fish (log+1) by year and depth. Year and depth were fixed factors and site was random. Significance was assessed using Type II Wald F tests with Kenward-Roger degrees if freedom (residual df=190). P-values for multiple comparisons were adjusted using the Tukey method. Multiple comparisons between years were averaged over depth.

	df	Sum Sq	Mean Sq	F-value	p
Year	4	3.7269	0.93174	13.1327	<0.001
Depth	1	0.2708	0.27081	3.8170	0.052
Year*Depth	4	0.2141	0.05351	0.7543	0.556

Pair	Diff	T ratio	p-adj
2015-2016	0.1139	2.059	0.2425
2015-2017	0.2939	5.318	<0.0001
2015-2019	0.2102	3.804	0.0018
2015-2023	0.3552	6.427	<0.0001
2016-2017	0.1800	3.253	0.0117
2016-2019	0.0963	1.741	0.4113
2016-2023	0.2413	4.362	0.0002
2017-2019	0.0837	-1.514	0.5549
2017-2023	0.0613	1.110	0.8013
2019-2023	0.1450	2.623	0.0702

Table C.4. Eigenvectors from the PCA for 2015 and 2019/23. Component loadings are scaled proportional to eigenvalues.

Stressors-2015	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**
Impervious Surface	1.2012	-0.06703	0.001629	-0.38561	-0.2281	-0.67092
OSDS	1.1469	-0.05108	0.013417	0.72641	0.2446	0.42346
Nutrients	1.1787	0.43256	-0.30458	0.3139	-0.43	-0.05262
Sediment	0.272	-0.53501	1.302574	0.00471	-0.3509	0.11424
Wave Energy	-0.6792	0.96289	0.052406	0.221	-0.8253	0.09181
Total Herbivores	0.6702	0.88202	0.163831	-0.80538	0.1813	0.51809
Herbivores-scrapers	-0.1491	1.08955	0.582318	0.34469	0.5784	-0.44497
Eigenvalue	2.3386	1.5303	0.9793	0.722	0.66626	0.50824
Prop. Explained	0.3341	0.2186	0.1399	0.1031	0.09518	0.07261
Cum. Prop.	0.3341	0.5527	0.6926	0.7958	0.89093	0.96354

Stressors-2019/23	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**
Impervious Surface	1.1429	-0.2045	0.35676	-0.7102	0.18931	0.28056
OSDS	1.1369	-0.3766	0.02094	0.4151	-0.68071	-0.33800
Nutrients	1.1822	0.1433	0.62129	0.3842	0.15255	0.29609

Sediment	-0.1919	-1.1549	-0.51993	0.4362	-0.05458	0.60465
Wave Energy	-0.6172	1.0341	0.50254	0.1822	-0.48061	0.46039
Total Herbivores	0.6050	0.6101	-0.99410	-0.5375	-0.32429	0.20521
Herbivores-scrapers	0.6055	0.8920	-0.58508	0.6719	0.43976	-0.01715
Eigenvalue	2.3352	1.7130	1.0741	0.8114	0.40863	0.17900
Prop. Explained	0.3336	0.2447	0.1534	0.1159	0.05838	0.02557
Cum. Prop.	0.3336	0.5783	0.7318	0.8477	0.97443	1.00000