



Changes in fish assemblages after marine heatwave events in West Hawai'i Island

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ABSTRACT: Marine heatwaves are prolonged events of anomalously warm water that affect diverse marine habitats and their associated biota. Evidence shows that anthropogenic climate change is increasing the frequency and duration of marine heatwaves and that coral reef systems are sensitive to the thermal stress imposed by these heatwaves. In this study, we examined fish community response to consecutive marine heatwaves (2014–2015) by analyzing changes in fish assemblages in Hawai'i over 11 yr (2009–2019). Subtidal video survey data were collected in 3 areas on the west side of the Big Island of Hawai'i. Fish were counted and identified to species or genus, then assigned to one of 7 functional groups: predators, secondary consumers, planktivores, corallivores, scrapers, grazers or browsers. Our study revealed 4 key findings. We show that all fish assemblages changed significantly in each area after the marine heatwaves. Across all 3 areas, the 3 most abundant functional groups (planktivores, grazers and secondary consumers) drove the observed changes in the community. Following the marine heatwaves, fish abundance increased in 2 areas with fewer fishing regulations. In the most protected area, fish abundance remained high and diversity indices were significantly higher post-marine heatwaves. Our results support the hypothesis that marine heatwaves can cause shifts in fish assemblages and that the precise nature of these shifts can vary over relatively short spatial scales that may coincide with scales of management.

KEY WORDS: Thermal stress · Fish biodiversity · Bleaching · Coral reef · Functional groups · Disturbance · Community ecology

1. INTRODUCTION

Extreme heatwave events have direct and indirect impacts on shallow nearshore communities, including but not limited to species range shifts, local extinctions, and fisheries-related economic impacts (Munday 2004, Perry et al. 2005, Smale et al. 2019). Marine heatwaves have been defined as discrete, prolonged, anomalously warm-water events that last 5 or more days, with surface temperatures higher than the 90th percentile based on a 30 yr historical baseline period in a particular location (Hobday et al. 2016). It has been reported that on average between

1925–1954 and 1987–2016, global marine heatwave frequency and duration increased by 34 and 17%, respectively (Oliver et al. 2018). Increasing frequency and duration of marine heatwave events is particularly stressful to ecosystems sensitive to elevated temperatures such as coral reefs, which occupy habitats with water temperatures close to their upper thermal limit (Spalding & Brown 2015).

Thermal stress in coral reefs can be measured in degree heating weeks, which consider the magnitude and duration of anomalously high temperatures for a 12 wk period in a specified area (Kayanne 2017). After 4 wk of thermal stress, substantial

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bleaching can occur, and at 8 wk, coral mortality can be expected (Coral Reef Watch 2015). Elevated ocean temperatures have caused worldwide bleaching events in the last few decades, leading to mass coral mortality in many regions and have been cited as a major—if not the most important—contributor to coral mortality (Hoegh-Guldberg 1999, Hughes et al. 2018a,b, Pratchett et al. 2018). Corals are the framework of coral reef ecosystems, and coral mortality and associated degradation has profound impacts on all other reef organisms who use and depend on these ecosystems.

Habitat degradation has indirect implications for coral reef fish, such as changes in fish assemblage composition (Jones & Syms 1998, Munday 2004, Hempson et al. 2017). Studies in Kimbe Bay, Papua New Guinea, reported declines in fish diversity of ~22% in areas after a coral mortality event caused by a marine heatwave, regardless of protection status (Jones et al. 2004). Research in Mafia Island Marine Park, Tanzania, reported significant increases in herbivores and a decrease in coral dwellers after a bleaching event (Garpe et al. 2006). Changes in fish assemblages can lead to changes in functional groups, which are determined by a combination of life history characteristics and trophic level (Graham et al. 2015). Functional groups reflect how these fish feed, what they consume and their impact on the substratum (Green & Bellwood 2009), and community changes can influence the ability of reefs to tolerate pulse perturbations associated with climate change (Hughes et al. 2007).

Coral reef ecosystems are not only subject to global climate change impacts but also local stressors such as land-based nutrient and pollution inputs, overfishing, growing human population, destruction of habitat and movement away from traditional conservation practices (i.e. spiritual and cultural beliefs) towards modern day exploitation (Friedlander 2018, Friedlander et al. 2003, Hughes et al. 2003, Abaya et al. 2018, MacNeil et al. 2019). Due to these multiple stressors, resilience is key for species' persistence. Resilience in this context refers to (1) the ability of a system to absorb shocks or pulse perturbations while still functioning in the same way, (2) the capacity for recovery following a disturbance and (3) the degree to which a system can adapt to new conditions (Holling 1973, Nyström et al. 2000, Bernhardt & Leslie 2013). Resilience-based management strategies have increasingly become of interest, as they offer a proactive versus reactive approach (Hughes et al. 2007) and use targeted decision making that reduces local human threats while managing systems and pro-

cesses that encourage resistance and recovery (Graham et al. 2013).

In this study, we examined subtidal reef fish diversity and abundance after consecutive marine heatwaves and corresponding bleaching events in Hawai'i to better understand the resilience of fish assemblages to marine heatwaves. Coral reefs and associated fish communities provide important ecosystem goods and services such as fisheries, research, tourism and aesthetic and cultural value (Bellwood et al. 2004, Friedlander et al. 2005, Marshall et al. 2019). For example, the economic value of healthy Hawaiian coral reefs is estimated to be US \$33.57 billion (Bishop et al. 2011). Coral reefs are especially important in sustaining cultural and traditional practices in the Hawaiian culture, as native Hawaiian people have relied upon marine resources for food security for many generations (Kittinger et al. 2015). It has been predicted that mass coral bleaching could become an annual event in Hawai'i as early as 2035, which could severely impact fisheries, the economy and local ways of life (Van Hooidonk et al. 2016).

In spring 2014, the first of several marine heatwaves was reported by the NOAA Coral Reef Watch program in the Hawaiian Archipelago. Multiple weeks of high sea surface temperature anomalies caused severe thermal stress in coral reef ecosystems throughout the islands (Social Science Research Institute 2017). NOAA defines the maximum monthly mean temperature for the main Hawaiian Islands to be 27°C, with a bleaching threshold of 28°C (Glynn & D'Croz 1990, Coral Reef Watch 2015, Jokiel et al. 2015). In 2014, NOAA's Coral Reef Watch Program reported the bleaching threshold temperature was exceeded for 8 wk, and in 2015, 12 wk of abnormally high temperatures caused severe coral bleaching across the state (Social Science Research Institute 2017). On average, 50% loss of coral cover was estimated along the west coast of Hawai'i Island, henceforth referred to as 'West Hawai'i' (Coral Reef Watch 2015, Social Science Research Institute 2017).

We analyzed 11 yr of subtidal video survey data spanning periods before, during and after the first marine heatwave event in 2014. We examined fish assemblages and used the relative abundance of functional groups and the species driving change within these groups as indicators of resilience (Bellwood et al. 2004). The 7 functional groups consisted of predators, secondary consumers, planktivores, corallivores and 3 herbivores: scrapers, grazers and browsers. The goals of this study were to (1) investigate changes in relative abundance of reef fish before, during and

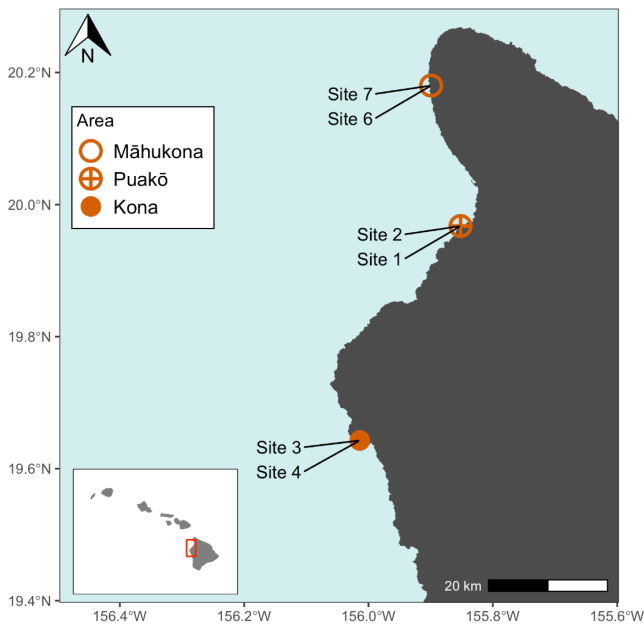


Fig. 1. Reef sites surveyed in West Hawai'i (Big Island, USA) from 2009–2019. Survey locations encompassed 2 sites (6 and 7) in Māhukona, 2 sites (1 and 2) in Puakō and 2 sites (3 and 4) in Kona. Symbols used for each area represent the level of fishing protection in those areas. Māhukona is managed under the West Hawai'i Fishery Management Area (least regulated/mostly open), Puakō is a Fish Replenishment Area (semi-closed) and Kona is a Marine Life Conservation District (most regulated/mostly closed)

after the marine heatwaves and (2) explore how changes in the relative abundance of fish functional groups influenced reef fish assemblages.

2. MATERIALS AND METHODS

2.1. Study area

We studied 6 reef sites located in 3 areas in West Hawai'i, USA (Fig. 1). All are within the West Hawai'i Regional Fishery Management Area which spans the entire western coastline of Hawai'i island (Hawai'i Administrative Rules, HAR 13-60.4; see Table S1 in the Supplement at www.int-res.com/articles/suppl/m698p095_supp.pdf for administrative rule details). The 2 sites in Māhukona are subject only to the regulations specified for the West Hawai'i Fishery Management Area, while the 2 sites in Puakō and 2 sites in Kona include additional management protections. Puakō is located within a Fish Replenishment Area (HAR 13-54). Kona is located within a Marine Life Conservation District (HAR 13-37). Prohibited activities in the Kona region are the most restrictive among

those in the 3 areas we studied. In 2013, a new rule was implemented that prohibited collection of fish, except those on a 'white list' of 40 species (for hobby aquarium purposes), within the entirety of the West Hawai'i Regional Fishery Management Area. In 2017, a moratorium on all aquarium fish collection was established across the entire region. For the purposes of this study, Māhukona is considered 'mostly open' to fishing, Puakō is 'semi-closed' to fishing, and Kona is 'mostly closed' to fishing. The 3 study areas also vary in levels of habitat complexity, oceanographic conditions, urbanization and human population (Table 1).

Surveys were conducted annually in late January and early February from 2009–2019. Survey locations encompassed 2 sites (i.e. transects) in each of 3 areas (Māhukona, Sites 6 and 7; Puakō Sites 1 and 2; Kona: Sites 3 and 4), for a total of 6 locations (Fig. 1, Table 1). Site 5 was sampled but not included in this analysis because the site is challenging to access in adverse conditions and was not consistently sampled. However, we have retained the original numbering of the sites (1–7) for consistency with the larger data set.

Transect initiation points were marked with GPS (Garmin eTrex HC series) locations. Unique underwater features were identified to ensure that each transect started and ended at the exact same points and ran along the exact same features every year. At Sites 1–4, transect location was determined by a vertical coral reef or rock/lava shelf extending for 100 m; at Site 6, location was determined by sand channels adjacent to reefs; and at Site 7, location was determined by an old mooring chain adjacent to reefs. Depth at the starting point and at each end of the transect was recorded.

2.2. Data collection and video transect analysis

Data were collected using underwater videos. Videos were recorded by pairs of trained scientific divers from the Seattle Aquarium using strip/belt transect survey methods (Larson et al. 2022). Transects were 100 m long and approximately 2 m wide, with the camera trained 1 m off the substrate; the total area sampled per transect was approximately 200 m². One diver operated the camera and the other laid the transect tape. Because 100 m of transect tape can be difficult to handle underwater, divers started in the center of the transect by swimming 50 m away from the starting point, then returned to the center and swam 50 m away from the starting point in a dif-

Table 1. Characteristics for each area

Characteristic	Māhukona	Puakō	Kona
Descriptive location	600 m north of Lapakahi State Park, a Marine Life Conservation District	Offshore of Puakō community	North of Kailua-Kona town
GPS	Site 6: 20° 11.003'N, 155° 54.124'W Site 7: 20° 11.043'N, 155° 54.901'W	Site 1: 19° 58.238'N, 155° 50.745'W Site 2: 19° 58.149' N, 155° 51.074'W	Site 3: 19° 38.753'N, 156° 1.002'W Site 4: 19° 38.684'N, 156° 0.967'W
Management	West Hawai'i Fishery Management Area	Fish Replenishment Area (FRA)	Marine Life Conservation District (MLCD)
Urban influence	Remote; <1000 residents (2016 census)	Small coastal residential community; <1000 residents (2016 census)	Town with residential and commercial occupancy; >13000 residents (2016 census)
Recreation	Adjacent bay and coral reef popular for authorized subsistence and recreational fishing, snorkel and dive tourism	Large, well-developed adjacent coral reef, popular for authorized subsistence and recreational fishing, snorkel and dive tourism	Nearshore coral reef is popular for authorized subsistence and recreational fishing, snorkel and shore diving tourism
Aerial	Sites 6 and 7 	Sites 1 and 2 	Sites 3 and 4 
Shore	West facing	North, northwest facing	Southwest facing
Distance from shore	Site 6: 81 m Site 7: 40 m	Site 1: 170 m Site 2: 130 m	Site 3: 100 m Site 4: 100 m
Depth	Site 6: 5.8–11.6 m Site 7: 2.4–8.2 m	Site 1: 6.1–7.9 m Site 2: 5.5–7.0 m	Site 3: 6.1–7 m Site 4: 5.2–6.4 m
Slope	0.05 %	0.04 %	0.08 %

ferent direction (see Table S2 for transect orientation). Data were collected on the forward or outbound section of the transect only. Transects were sampled once per year. The Māhukona sites were not surveyed in 2009 or 2015 due to poor conditions (see Table S3 for survey summary).

Camera systems were upgraded in 2011 (from standard-definition Sony VX2100 mini DV camera to high-definition Sony αNEX 5N) and 2015 (to Sony α5000) as higher quality video technology became available. Safety communication systems included wireless transceivers, microphone and earphones in full facemasks and a transceiver mounted to the underwater camera housing enabling the camera to record the divers speaking. Surveys were conducted between 10:00 and 15:00 h for consistency (light, fish behavior, visibility).

Videos were analyzed for fish diversity and abundance by Seattle Aquarium staff members using commercially available software (VLC Media Player v.3.0.8) and high-definition monitors. Count-

ing teams consisted of 2–3 staff members with professional expertise in Hawai'i reef fish identification from the same group of individuals that conducted the surveys. Fish were identified to species whenever possible or genus when we were unable to determine species (See Table S4 for list of all species).

The benthic environment was characterized by taking screenshots of each video and uploading them to the open-source software CoralNet (<https://coral-net.ucsd.edu>; Beijbom et al. 2015) for analysis. Forty frames evenly spaced per 100 m transect video were used, with 10 randomly distributed points in the lower 30 % per frame to focus on the benthos to compensate for the forward-facing camera view. Each point was classified as live coral, dead coral, sand, hard substrate, water, crustose coralline algae or unknown. Macroalgae were rarely seen and not included in this analysis. Percent cover per transect was calculated as the average of 40 frames along the transect.

2.3. Sea surface temperature data

Environmental data were downloaded from publicly available data sets from NOAA. Hourly sea surface temperature (°C) data were downloaded from historical NOAA Tides and Currents, Kawaihae Station (No. 1617433), and averaged per month and by year. The Hawai'i Division of Aquatic Resources (DAR) reported the first marine heatwave beginning in spring 2014 (Walsh et al. 2020). Because our surveys were conducted in January and February, calendar years 2015–2019 were considered post-heatwaves in this analysis. While high temperatures were still observed after 2015, the peak of the temperature anomaly, which occurred between our 2014 and 2015 surveys, divided the data into the 2 groups used in this analysis (pre-heatwaves: 2009–2014; post-heatwaves: 2015–2019).

2.4. Data analyses

All calculations were performed in R v.4.0.3 (R Core Team 2020) using the packages 'tidyverse' (Wickham et al. 2019), 'vegan' (Oksanen et al. 2020), 'cowplot' (Wilke 2020), 'patchwork' (Pedersen 2020), 'RcolorBrewer' (Neuwirth 2022) and 'MetBrewer' (Mills 2022). Level of significance was set at $\alpha = 0.05$. Fish species were categorized into 7 established functional groups: predators (carnivores), secondary consumers (omnivores), corallivores (rely on coral or coral polyps), planktivores (rely on plankton), browsers (reduce macroalgal cover), grazers (feed on algal turfs) and scrapers (remove algal turfs and open space for coral recruitment) (Graham et al. 2015, Donovan 2017). Trophic level and life history characteristics were checked against resources to aid in categorization of functional groups (Hobson 1974, Coral Reef Network 2005, Hoover 2008, DAR 2014, Donovan 2017).

Abundance data were non-normally distributed, so non-parametric tests of significance were used. Data were $\log(x + 1)$ transformed prior to analysis. Multivariate non-metric multidimensional scaling (NMDS) techniques were used to visually assess patterns of change in fish assemblage between the 3 study areas for years before (2009–2014) and after (2015–2019) the first marine heatwave. Ordinations were calculated with Bray-Curtis dissimilarity distance measures ('metaMDS', 'vegan' package). Each point represented the fish assemblage observed in that area in each year. Goodness of fit was indicated by the stress value (Clarke 1993). To identify which functional groups and species contributed most to the dissimilarity, a

similarity percentage procedure (SIMPER) was used to compute average dissimilarity between pairs of intergroup samples ('simper', 'vegan' package).

Multiple permutational analysis of variance (PERMANOVA) tests were used to examine whether fish assemblage structure differed before and after the first heatwave ('adonis', 'vegan' package). The 3 areas were first analyzed collectively and then separately because area was found to have a significant effect. The first collective model for all areas included sampling period (before and after bleaching) and area as fixed effects, with site nested within area as a random effect. Data were then separated by area and a model was run for each, with sampling period as a fixed effect and site as a random effect. PERMANOVA tests were performed for total abundance, then individually for all functional groups.

Species richness and the Shannon-Wiener (H') and Simpson (D) diversity indices (Hill 1973) were calculated for each site in each year ('diversity', 'vegan' package). Species richness is a measure of the number of unique species present. H' is a calculation of diversity in which communities of low diversity have values close to 0. This index is sensitive to species richness, so D was also calculated. D uses weighted arithmetic means and is less sensitive to richness. The complement to Simpson's D was calculated ($1 - \text{index}$), in which communities with low diversity have values close to 0, so H' and D comparisons could easily be made. Changes in H' and D diversity indices were assessed using nested, mixed-model ANOVA with factors for sampling period (fixed), area (fixed) and site (random, nested within area). Because area was found to have a significant effect, diversity indices were assessed at the area level, with period (fixed) and site (random) factors.

3. RESULTS

3.1. Data summary

Monthly average sea surface temperature ranged from a minimum of 24.2°C in March 2009 to a maximum of 29.8°C in September 2015 (Fig. 2, Table A1 in the Appendix). Seasonal fluctuations were observed, with low average temperatures of $26.1 \pm 0.7^\circ\text{C}$ in the winter months (Dec, Jan, Feb) and high average temperatures of $28.2 \pm 0.8^\circ\text{C}$ in fall months (Sept, Oct, November). The 28°C bleaching threshold was exceeded in both 2014 and 2015. Winter temperatures in early 2014 remained high, above 27.2°C, and the highest temperature anomaly of 29.8°C was

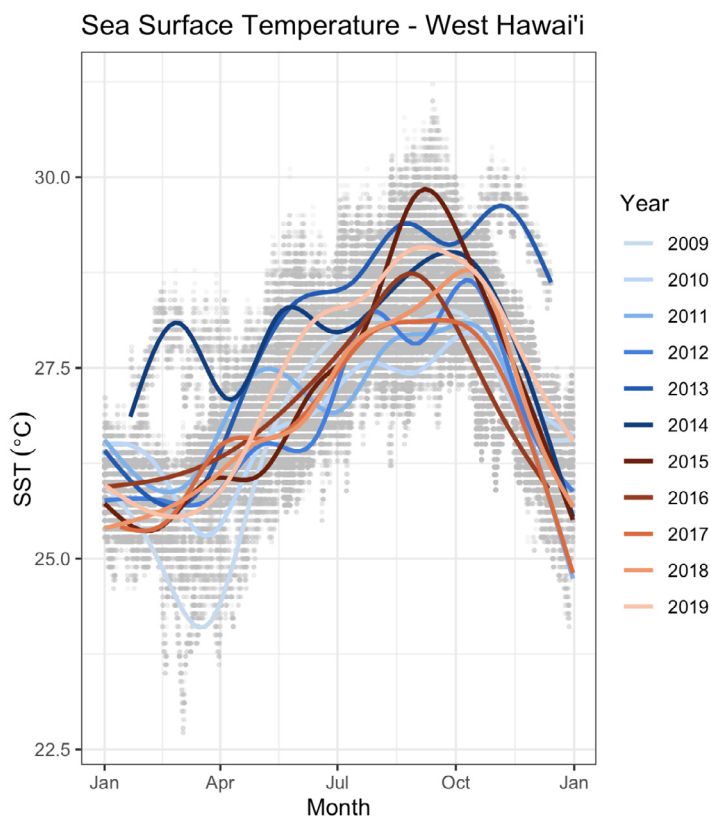


Fig. 2. Sea surface temperature (gray) with rolling monthly averages (colors) over the study period (2009–2019). Seasonally warm temperatures occurred in both pre-heatwaves (blues) and post-heatwaves (reds) years; however, peak temperature anomaly occurred in September 2015 (dark red)

observed in September 2015. Because our surveys were conducted in January and February, the temperature anomaly of March 2014 was not reflected in our data until the following year, hence separating the data from 2009–2014 and 2015–2019 for pre- and post-periods.

Data from 22 transects were analyzed from Kona and Puakō, and 16 transects were analyzed from Māhukona (Table S3). In all 3 areas after 2015, dead coral cover increased, live coral cover decreased and non-coral cover remained stable (Fig. 3, Table A2). Percent live coral cover ranged from 7.3% (Kona, 2016) to 24.1% (Puakō, 2011). Percent dead coral cover ranged from 5.9% (Māhukona, 2012) to 27.6% (Kona, 2016). Non-coral benthos (sand, hard substrate, water, crustose coralline algae) ranged from 1.7% (Puakō, 2011) to 10.6% (Māhukona, 2018). After the marine heatwaves, maximum dead coral cover was 27.6% in Kona in 2016, 15.7% in Māhukona in 2018 and 25.9% in Puakō in 2018.

A total of 114 species and 4 genera were identified among 25 006 individual fish (Tables 2 & S4 for list of all species). Among the 3 study areas, individuals from Māhukona made up 12.5% of the data set ($n = 3119$ fish), individuals from Puakō made up 27.8% ($n = 6955$ fish) and individuals from Kona made up 59.7% ($n = 14\,932$ fish). The most abundant fish species was *Chromis vanderbilti* (blackfin chromis), a planktivorous damselfish, with 5782 individuals



Fig. 3. Benthic composition for each pair of sites by area over the study period (2009–2019). Vertical dotted line divides the data into 2 groups: pre- (2009–2014) and post-marine heatwaves (2015–2019). Non-coral benthos includes sand, hard substrate, water or crustose coralline algae (yellow). Māhukona was not surveyed in 2009 and 2015

Table 2. Total fish counts and number of species by functional group for each area

Functional group (total species)	Total fish		Māhukona	Puakō	Kona
Predator (n = 12)	141	Species	5	6	9
		Fish counts	16	71	54
Secondary consumer (n = 60)	5841	Species	32	38	29
		Fish counts	1306	2340	2195
Corallivore (n = 7)	411	Species	6	6	5
		Fish counts	94	179	138
Planktivore (n = 15)	7396	Species	8	8	4
		Fish counts	716	1226	5454
Grazer (n = 14)	10091	Species	7	11	13
		Fish counts	892	2691	6508
Scraper (n = 5)	753	Species	3	5	4
		Fish counts	36	359	358
Browser (n = 5)	373	Species	3	2	5
		Fish counts	59	89	225
Total count (percent of total)	25006		3119 (12.5%)	6155 (27.8%)	14932 (59.7%)

recorded over the entire data set. The most frequently observed fish species was *Acanthurus nigrofuscus* (lavender tang), a grazer surgeonfish, present in 99% of transects. Grazers were the largest functional group (n = 10 091 fish), followed by planktivores (7396 fish), secondary consumers (5841 fish), scrapers (753 fish), corallivores (411 fish), browsers (373 fish) and predators (141 fish).

Fish assemblage composition by functional group changed after the first marine heatwave in all 3 study areas (Fig. 4). There was some shift in the distribution of points between pre- and post-heatwaves, as seen in the NMDS visualization; this difference was more evi-

dent for Puakō and Māhukona than Kona. The points representing Māhukona post-heatwaves moved towards the groupings of Puakō and Kona. In all 3 areas, within-area variability decreased post-heatwaves (i.e. the points have less spread). PERMANOVA results indicated that area explained 36% of the variance (pseudo- $F_{2,52} = 20.65$, $p < 0.01$) and period (pre- or post-heatwaves) explained 8.9% (pseudo- $F_{1,52} = 10.22$, $p < 0.001$). There was a significant area $\times$ period interaction which explained 5.4% of the variance (pseudo- $F_{2,52} = 3.12$, $p < 0.05$), so each area was then tested separately with PERMANOVA methods and is reported in each respective section below.

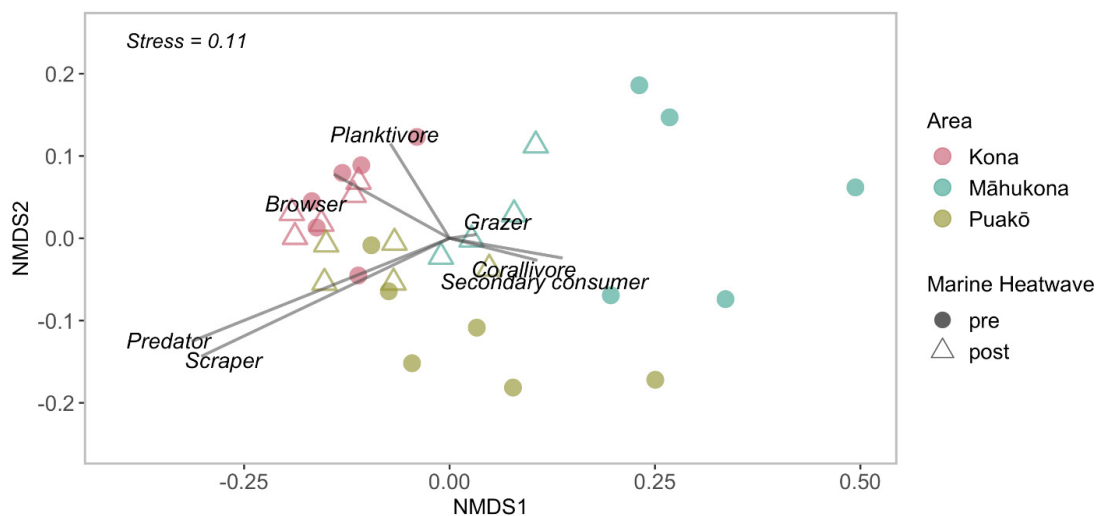


Fig. 4. Multivariate non-metric multidimensional scaling (NMDS) techniques used to assess patterns in changes of fish assemblage after marine heatwaves between 3 areas (by color) in West Hawai'i. Ordinations were calculated with Bray-Curtis dissimilarity distance measures on $\log(x + 1)$ -transformed data. Marine heatwave symbols designate periods before (2009–2014) and after (2015–2019) the first heatwave occurred

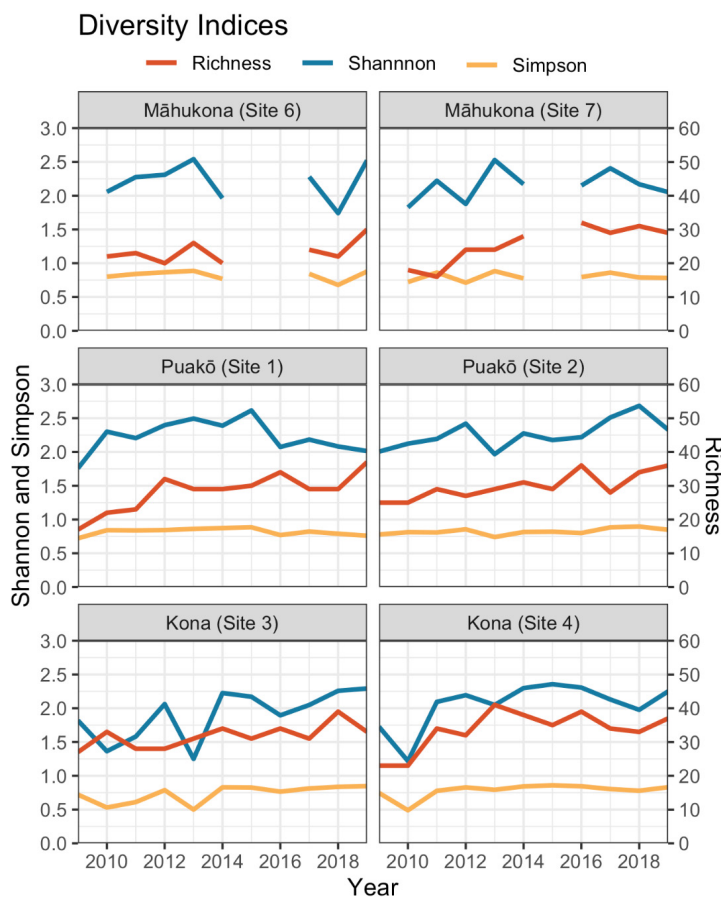


Fig. 5. Shannon-Wiener and Simpson diversity indices and species richness calculations for each pair of sites by area over the study period (2009–2019). Māhukona was not surveyed in 2009 and 2015

Diversity indices (H' , D and richness) were calculated for all 6 sites (Fig. 5). H' values ranged from a minimum of 1.22 to a maximum of 2.68, D ranged from 0.49 to 0.90 and species richness ranged from 16 to 41 across all sites. Over the study period, H' values were variable, while D and richness remained more stable. When testing all sites together, H' and D indices increased significantly following the marine heatwaves (nested, mixed-model ANOVA, $F_{1,52} = 5.004$, $p < 0.05$ and $F_{1,52} = 4.808$, $p < 0.05$, respectively). Area was significant for H' values ($F_{2,52} = 5.926$, $p < 0.05$), while area and the period $\times$ area interaction were significant for D values ($F_{2,52} = 4.285$, $p < 0.05$ and $F_{3,52} = 3.840$, $p < 0.05$, respectively). Richness values were significantly higher following the marine heatwaves (nested, mixed-model ANOVA, $F_{1,52} = 24.419$, $p < 0.001$), and area was also found to be a significant factor (nested, mixed-model ANOVA, $F_{2,52} = 17.353$, $p < 0.001$).

3.2. Māhukona

Fish abundance in Māhukona ranged from a minimum of 127 fish in 2011 to a maximum of 682 fish in 2019 (Fig. 6). In total, 64 distinct species were observed in this area over the study period. All years surveyed after the marine heatwaves showed higher total abundance than years prior. The relative abundance of functional groups was significantly different post-heatwaves (PERMANOVA pseudo- $F_{1,14} = 5.12$, $p < 0.01$), and a dummy variable dividing the data into 2 groups (pre- and post-heatwaves) explained 25.3% of the variance in the data. Site accounted for 5.5% of the variance (PERMANOVA pseudo- $F_{1,14} = 1.12$, $p < 0.05$). Fish assemblage by species was significantly different post-heatwaves (PERMANOVA pseudo- $F_{1,14} = 3.12$, $p < 0.001$), and the heatwave variable explained 15.5% of the variance while site explained 14.8% of the variance (PERMANOVA pseudo- $F_{1,14} = 2.98$, $p < 0.001$, data not shown).

The largest functional groups by abundance were secondary consumers, followed by grazers and planktivores (Fig. 7), together accounting for 93.4% of the fish observed at Māhukona. Species within the grazers and secondary consumers were significantly different post-heatwaves (Table 3, see Fig. S1 for all functional groups). In total, 63 species accounted for 99% of the difference post-heatwaves, with increases in *Acanthurus olivaceus* (orange shoulder tang, grazer) contributing most of the change (SIMPER, $p < 0.05$).

Diversity index values (H' and D , respectively) ranged from a minimum of 1.74 and 0.68 to a maximum of 2.54 and 0.89. Species richness ranged from 16–32. Māhukona had the lowest richness values compared to the other 2 areas and the smallest change in diversity values over the study period (Fig. 5). H' and D indices were not significantly different following the marine heatwaves (nested, mixed-model ANOVA, $F_{1,14} = 0.010$, $p = 0.923$ and $F_{1,14} = 0.059$, $p = 0.812$, respectively). Richness values were significantly higher following the marine heatwaves (nested, mixed-model ANOVA, $F_{1,14} = 11.147$, $p < 0.01$).

3.3. Puakō

Abundance of fish in Puakō ranged from a minimum of 296 fish counted in 2010 to a maximum of 1219 fish

Abundance by Area

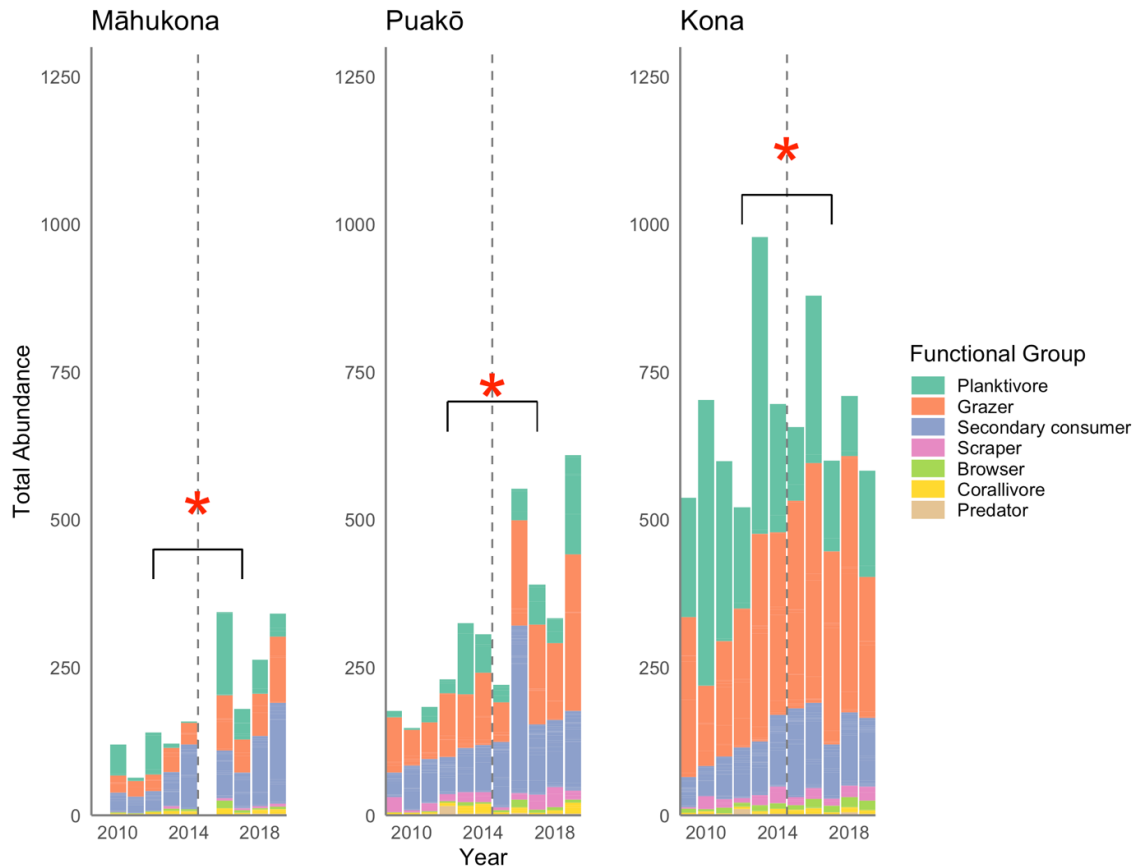


Fig. 6. Transect-averaged fish abundance and assemblage for all 3 areas over the study period (2009–2019). The vertical dotted line divides the data into 2 groups: pre- (2009–2014) and post-marine heatwaves (2015–2019). Red asterisks: significant changes in fish assemblage after the marine heatwaves (PERMANOVA, $p < 0.05$). Functional groups are identified by colors

in 2019 (Fig. 6). A total of 76 distinct species were observed in this area over the study period. The relative abundance of functional groups was significantly different post-heatwaves (PERMANOVA pseudo- $F_{1,19} = 4.56$, $p < 0.01$), and a dummy variable dividing the data into 2 groups (pre- and post-heatwaves) explained 18.1% of the variance in the data. Site explained

6.5% of the variance (PERMANOVA pseudo- $F_{1,19} = 1.65$, $p < 0.01$). Fish assemblage by species was also significantly different post-heatwaves (PERMANOVA pseudo- $F_{1,19} = 2.87$, $p < 0.001$), and the heatwave variable explained 12.3% of the variance while site explained 6.5% of the variance (PERMANOVA pseudo- $F_{1,19} = 1.51$, $p < 0.001$, data not shown).

Table 3. PERMANOVA results for each functional group per area. **Bold** values are significantly different post-marine heatwaves ($p < 0.05$)

Functional group	Māhukona	Puakō	Kona
Grazer	$F_{1,15} = 7.49$, $p < 0.001$	$F_{1,20} = 3.19$, $p < 0.01$	$F_{1,20} = 1.42$, $p < 0.05$
Planktivore	$F_{1,13} = 0.66$, $p = 0.573$	$F_{1,20} = 3.94$, $p < 0.01$	$F_{1,20} = 6.13$, $p < 0.05$
Secondary consumer	$F_{1,15} = 2.84$, $p < 0.05$	$F_{1,20} = 3.52$, $p < 0.001$	$F_{1,20} = 2.86$, $p < 0.01$
Scraper	$F_{1,8} = 1.13$, $p = 0.59$	$F_{1,20} = -0.06$, $p = 0.96$	$F_{1,20} = -0.06$, $p = 0.96$
Corallivore	$F_{1,15} = 0.73$, $p = 0.59$	$F_{1,20} = -0.04$, $p = 0.97$	$F_{1,20} = 1.30$, $p = 0.26$
Browser	$F_{1,14} = 1.14$, $p = 0.35$	$F_{1,16} = 2.09$, $p = 0.16$	$F_{1,20} = 3.62$, $p < 0.05$
Predator	$F_{1,5} = 2.80$, $p = 0.20$	$F_{1,5} = 2.80$, $p = 0.20$	$F_{1,15} = 0.67$, $p = 0.65$

Top Three Functional Groups by Area

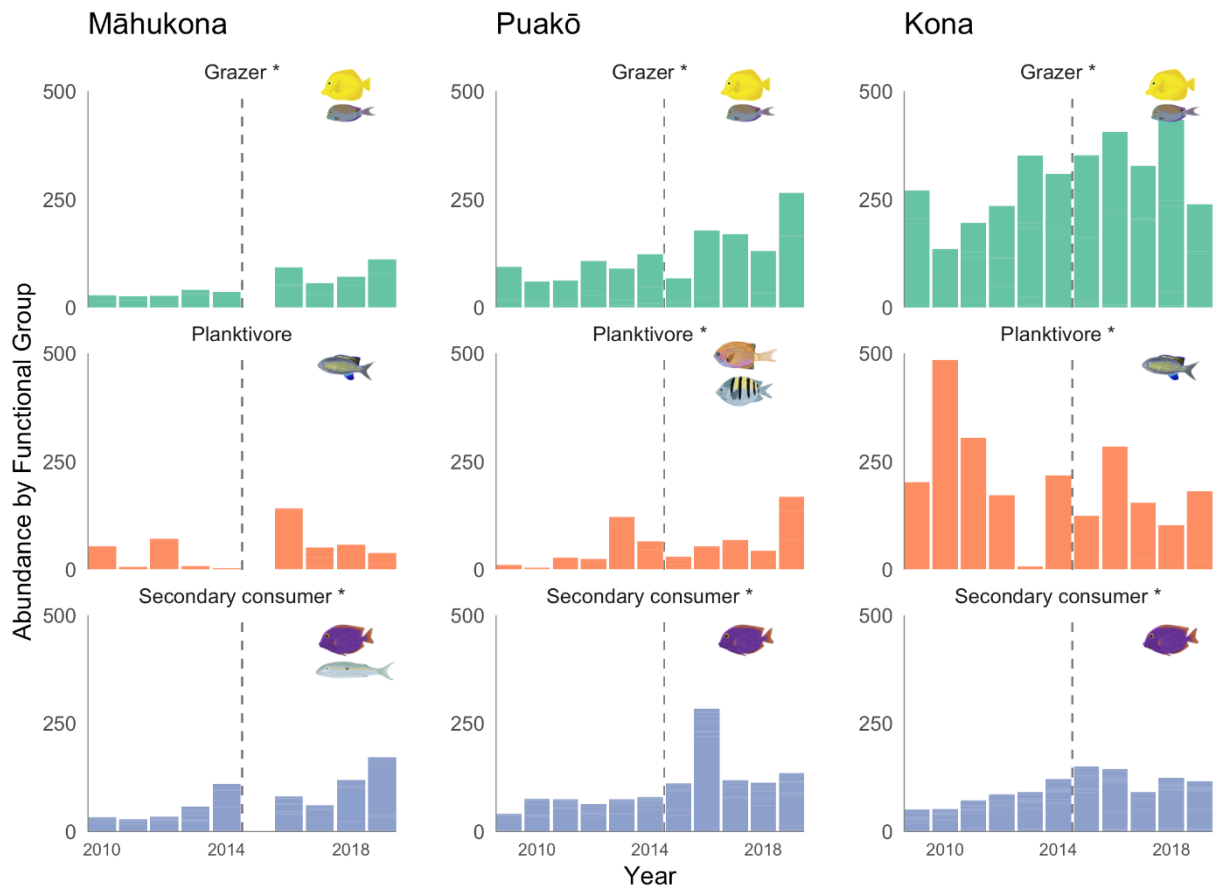


Fig. 7. Top 3 functional groups for all 3 sites over the study period (2009–2019). The vertical dotted line divides the data into 2 periods: pre- and post-marine heatwaves. Asterisks: significant change in functional group makeup after the marine heatwaves (PERMANOVA, $p < 0.05$). The most abundant species within each of these functional groups are indicated within each panel: yellow tang *Zebrasoma flavescens* and lavender tang *Acanthurus nigrofusus* in the grazer category for Māhukona (34.1, 56.5%), Puakō (66.1, 27.0%) and Kona (42.2, 39.7% respectively); blackfin chromis *Chromis vanderbilti* in the planktivore category for Māhukona (74.4%) and Kona (94.8%); Agile chromis *C. agilis* and Hawaiian sergeant *Abudefduf abdominalis* in the planktivore category for Puakō (29.1 and 53.4%, respectively); Goldrim (kole) tang *Ctenochaetus strigosus* and yellow stripe goatfish *Mulloidichthys flavolineatus* in the secondary consumer category for Māhukona (30.8, 37.0% respectively); and Goldrim (kole) tang *C. strigosus* in the secondary consumer category for Puakō (50.6%) and Kona (44.0%)

The largest functional groups by abundance were grazers, followed by secondary consumers and planktivores (Fig. 7), accounting for 90% of the observations at Puakō. Species within the grazer, planktivore and secondary consumer functional groups were significantly different post-heatwaves (Table 3, see Fig. S1 for all functional groups). A total of 74 fish species accounted for 99% of the difference post-heatwaves, with increases in *Chromis agilis* (agile chromis, planktivore) contributing most of the change (SIMPER, $p < 0.001$).

Diversity index values (H' and D , respectively) ranged from a minimum of 1.76 and 0.72 to a maximum of 2.68 and 0.90. Species richness ranged from 17 to 37. The Puakō sites showed the most stability in diversity indices and largest change in richness val-

ues across the study period, indicating the addition of new species to the area (Fig. 5). H' and D indices were not significantly different following the marine heatwaves (nested, mixed-model ANOVA, $F_{1,19} = 0.617$, $p = 0.442$ and $F_{1,19} = 0.296$, $p = 0.593$, respectively). Richness values were significantly higher following the marine heatwaves (nested, mixed-model ANOVA, $F_{1,19} = 11.229$, $p < 0.01$).

3.4. Kona

Abundance of fish in Kona ranged from a minimum of 1043 fish counted in 2012 to a maximum of 1957 fish in 2013 (Fig. 6); 69 distinct species were observed

in this area over the study period. The relative abundance of functional groups was significantly different pre- and post-heatwave periods (PERMANOVA pseudo- $F_{1,19} = 4.19$, $p < 0.01$), and a dummy variable dividing the data into 2 groups (pre- and post-heatwaves) explained 16.0% of the variance in the data. Site explained 11.4% of the variance (PERMANOVA pseudo- $F_{1,19} = 3.00$, $p < 0.01$). Fish assemblage by species was also significantly different post-heatwaves (PERMANOVA pseudo- $F_{1,19} = 3.17$, $p < 0.01$), and the heatwave variable explained 11.9% of the variance while site explained 16.6% of the variance (PERMANOVA pseudo- $F_{1,19} = 4.40$, $p < 0.01$, data not shown).

The largest functional groups by abundance were grazers, followed by planktivores and secondary consumers (Fig. 7), together accounting for 94.8% of the observations at Kona. Species within the grazers, planktivores, secondary consumer and browser functional groups were significantly different post-heatwaves (Table 3, see Supplementary Fig. S1 for all functional groups). In total, 68 fish species accounted for 99% of the difference post-heatwaves, with increases in *Abudefduf abdominalis* (Hawaiian sergeant, planktivore) contributing most of the change (SIMPER, $p < 0.05$).

Diversity index values (H' and D , respectively) ranged from a minimum of 1.21 and 0.49 to a maximum of 2.36 and 0.86. Species richness ranged from 23–41. The Kona sites showed more variability in H' prior to the marine heatwaves, with more stability in the years after the heatwaves. H' and D indices were significantly higher following the marine heatwaves (nested, mixed-model ANOVA, $F_{1,19} = 6.958$, $p < 0.05$ and $F_{1,19} = 7.125$, $p < 0.05$, respectively). Richness values were not significantly different following the marine heatwaves (nested, mixed-model ANOVA, $F_{1,19} = 3.424$, $p = 0.08$). Diversity indices also showed the largest increase in values over the study period, indicating more change in the number of total species and rare species in this area compared to the other 2 areas (Fig. 5).

4. DISCUSSION

Our study of the response of fish assemblages to marine heatwave events across 3 areas in West Hawai'i revealed 4 key findings. All fish assemblages changed significantly after the marine heatwaves. Across all 3 areas, the 3 most abundant functional groups (grazers, planktivores and secondary consumers) drove the observed changes in the community. Total fish abundance increased in years after the marine heatwaves in the areas with fewer fishing

regulations. In the most protected area, fish abundance remained high, and diversity indices were significantly higher post-marine heatwaves.

4.1. Abundance

The increase and stability in fish abundance seen in our data after the marine heatwaves challenges an assumption that coral bleaching leads to a net loss of coral-dependent reef fish (Jones et al. 2004, Pratchett et al. 2011, Wismer et al. 2019). The 2 areas more open to fishing, Māhukona and Puakō, showed increases in fish abundance post-marine heatwaves, while fish abundance in Kona, the area mostly closed to fishing and with the highest percent of coral bleaching, remained high and relatively stable throughout the study period.

Of particular interest in this study was that fish abundance in Kona, the most protected area, was 2–3 times higher than that of Māhukona and Puakō. It may be that fish species in Kona are closer to carrying capacity (i.e. the equilibrium value of the logistic model of population growth; Odum & Barrett 1971) than those exposed to higher fishing pressure and hence less likely to show changes or increases in abundance following disturbance. The data also showed evidence for habitat shifts, where small-bodied grazing fish moved into areas with degraded habitat. Reductions in live coral cover reportedly increase algal resource availability (Rogers et al. 2018), which can attract grazers to an area.

It is unknown whether the increases in fish abundance reported here can be sustained over time. For example, at Lizard Island, Australia, coral cover declined by 72–83% after a bleaching event and was associated with a 71% increase in fish biomass, 41% increase in productivity and 37% increase in consumed biomass (Morais et al. 2020). Those authors suggest that fish biomass replacement levels may not be sustainable following loss of coral cover and that changes in biomass that initially appear favorable may not be stable over time. It is unclear from our data whether the shifts in fish abundance on the West Hawai'i reefs will persist; only continued long-term monitoring will determine where the reefs can support higher fish biomass levels over the long term.

4.2. Functional groups

Fish assemblages were significantly different in the years after the marine heatwaves across all 3

areas. Consistent with previous studies, there was a significant shift towards algae-farming, small-bodied, habitat-generalist fish (Adam et al. 2011, Gilmour et al. 2013, Ceccarelli et al. 2016, Rogers et al. 2018, Robinson et al. 2019, Morais et al. 2020). Climate change favors generalist consumers, which replace specialist species that cannot adapt to changing environments (Richardson et al. 2018). The 3 species contributing the most to the change reported here were *Acanthurus olivaceus* (orange shoulder tang, grazer), *Chromis agilis* (agile chromis, planktivore) and *Abudefduf abdominalis* (Hawaiian sergeant, planktivore). Notably, 2 of these species are planktivores, suggesting that the effects of the marine heatwaves extended beyond the benthic community.

4.3. Diversity

We found significant increases in diversity at the sites in Kona following the marine heatwaves. This area also had the highest proportion of coral death observations, and previous work has shown positive effects on the local diversity of reef fishes with moderate levels of coral loss (Pratchett et al. 2018). Māhukona and Puakō did not exhibit statistically significant changes in diversity, although species richness was found to be significantly higher for both areas after the marine heatwaves (richness in Kona was not statistically significant). Our data did not allow for testing the effects of management status. However, we note that regulations were established (specifically, the aquarium ‘white list’ in 2013) to protect more rare species and restrict collection by the hobbyist aquarium fish trade. The moratorium on aquarium fish collection in 2017 also likely influenced rare species abundances.

4.4. Limitations

We acknowledge limitations in our study with respect to sampling design. The 3 areas sampled differed in terms of management regime, but our design did not allow us to test for the effect of management status. Moreover, surveys were performed once per year, which does not allow us to capture temporal or seasonal variation that may have occurred. Only fish larger than 4–5 mm are captured on the camera and can be identified upon viewing the video; cryptobenthic and juvenile fish are not easily observed. Finally, size and age estimates were not recorded in this study, and only presence or absence was docu-

mented. Despite these limitations, archived video footage allowed us to consistently enumerate fish and invertebrate species over repeated sampling events.

4.5. Management considerations

It is important to consider the history and trajectories of change in West Hawai‘i to avoid the problem of shifting baselines. For instance, declines in coral cover and fish abundance have been reported from Puakō over the last 40 yr (Walsh et al. 2018). Studies conducted in 2007–2008 (Walsh et al. 2018) found significant declines in fish abundance compared to reference studies in 1978–1981 (Hayes et al. 1982). While we observed increases in total fish abundance over the 11 yr study period, these estimates likely are lower than historical abundance estimates. The historical data were collected using different methods and are not comparable to our data. However, general trends reported by Walsh et al. (2018) described the following: 36% decline in piscivores, 46% decline in planktivores, 49% decline in invertivores and 57% decline in herbivores/detrivores compared to historical levels. Additional protective management measures may be required to rebuild coral and reef fish populations to historical abundance levels (Walsh et al. 2018).

The sites in Kona, located within the Old Kona Airport Marine Life Conservation District with the highest level of fishing protection among our sites, showed the highest total fish abundance and least temporal variation in abundance over the study period. These sites had the highest abundance and diversity values despite having the highest percent loss of coral cover. While the fish assemblage was significantly different after the marine heatwaves (decreases in reef-dwelling planktivore species and increases in grazer and secondary consumer species), the fact that fish abundance remained high could suggest more stability in response to new or unusual environmental conditions (Bernhardt & Leslie 2013).

Marine protected areas can be an effective strategy to (1) help manage local stressors such as overfishing, (2) protect key species and (3) provide a refuge for life stages that are more sensitive, but they do not protect against sea surface warming or coral bleaching (Hughes et al. 2018a, Johnson et al. 2022). Meta-analysis revealed that marine protected areas had no general effect on coral loss or post-disturbance recovery (Pratchett et al. 2018, Bruno et al.

2019). This finding is consistent with our observation that sites within the Marine Life Conservation District had the highest levels of coral loss following the marine heatwaves. Similar to studies conducted in the Florida Keys (Kramer & Heck 2007), high coral loss occurred while abundances of herbivore fish remained high. Bruno et al. (2019) emphasized that local management strategies such as protected areas and fishery restrictions alone are not enough to improve reef resilience and stated that directly addressing anthropogenic climate change is the solution. Our observations are relevant to management actions that could be taken by the state of Hawai'i and the Department of Land and Natural Resources (DLNR) to effectively manage 30% of Hawai'i's nearshore waters by 2030, as specified in the Sustainable Hawai'i Initiative of 2016.

Our work shows that changes to fish assemblages caused by marine heatwaves can vary over relatively short spatial scales that may coincide with scales of management. Disentangling the effects of thermal stress from those of management regimes will help to clarify practical actions that could be taken in the face of warming waters.

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Appendix.

Table A1. Sea surface temperature (°C) Summary for West Hawai'i from 2009–2019. Hourly sea surface temperature data were downloaded from historical NOAA Tides and Currents, Kawaihae Station (No. 1617433) and averaged per month and by year

Year	Min.	Max.	Mean	SD
2009	22.7	29.5	26.7	1.45
2010	24.2	29.1	26.9	0.85
2011	24.1	29.1	27.1	0.86
2012	24.9	29.6	26.9	1.08
2013	24.5	30.8	28.0	1.46
2014	25.5	30.1	28.0	0.87
2015	24.7	31.2	27.2	1.50
2016	25.1	30.1	27.3	0.95
2017	24.7	29.8	27.2	0.88
2018	24.6	30.1	27.4	1.01
2019	25.7	30.4	28.0	0.99

Table A2. Changes in percentage of benthic composition across 3 areas in West Hawai'i from 2009–2019

Area	Benthos type	Min. (year)	Max. (year)	Mean
Māhukona	Live coral	7.55 (2018)	16.75 (2010)	12.29
	Dead coral	5.90 (2012)	15.65 (2018)	10.99
	Non-coral	7.18 (2010)	10.64 (2018)	9.47
Puakō	Live coral	11.05 (2018)	24.05 (2011)	19.16
	Dead coral	10.15 (2011)	25.85 (2018)	15.37
	Non-coral	1.69 (2011)	3.23 (2012)	2.48
Kona	Live coral	7.30 (2016)	13.40 (2010 & 2014)	10.66
	Dead coral	16.24 (2010)	27.62 (2016)	21.46
	Non-coral	2.88 (2011)	5.13 (2009)	4.19

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