Fish Assemblage Structure Before and After a Marine Heatwave in West Hawai'i

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

Master of Marine Affairs

University of Washington
2021

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Program Authorized to Offer Degree:
School of Marine and Environmental Affairs

University of Washington

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Coral reefs are subject to marine heatwaves caused by human-induced climate change. Long-term thermal stress can negatively affect corals and the associated marine organisms that use these areas as critical habitat. In this study, we examined coral reef resilience to climate change by analyzing changes in fish assemblages following a marine heatwave. We analyzed 11 years of subtidal video survey data in three areas in West Hawai'i, capturing a marine heatwave event from 2014 - 2016. Fish were counted and identified to species, then assigned to one of seven functional groups: predators, secondary consumers, planktivores, corallivores, scrapers, grazers and browsers. Our study revealed three key findings. First, we show that regardless of habitat differences and management strategy, all fish assemblages became more homogeneous after a major marine heatwave. Second, we found that only eight species drove most of the changes in functional groups across locations. Third, following the marine heatwave, fish abundance increased in the areas with fewer fishing regulations, and appeared to remain high and relatively stable in a more protected area. Understanding how marine heatwaves impact coral reef communities can guide decision-making for effective coastal management. Continued long term monitoring is necessary to evaluate disturbance impacts on the coral reef ecosystem as climate change and marine heatwaves are anticipated to continue into the future.

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We have no known conflict of interest to disclose.

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Abstract

Coral reefs are subject to marine heatwaves caused by human-induced climate change. Long-term thermal stress can negatively affect corals and the associated marine organisms that use these areas as critical habitat. In this study, we examined coral reef resilience to climate change by analyzing changes in fish assemblages following a marine heatwave. We analyzed 11 years of subtidal video survey data in three areas in West Hawai'i, capturing a marine heatwave event from 2014 - 2016. Fish were counted and identified to species, then assigned to one of seven functional groups: predators, secondary consumers, planktivores, corallivores, scrapers, grazers and browsers. Our study revealed three key findings. First, we show that regardless of habitat differences and management strategy, all fish assemblages became more homogeneous after a major marine heatwave. Second, we found that only eight species drove most of the changes in functional groups across locations. Third, following the marine heatwave, fish abundance increased in the areas with fewer fishing regulations, and appeared to remain high and relatively stable in a more protected area. Understanding how marine heatwaves impact coral reef communities can guide decision-making for effective coastal management. Continued long term monitoring is necessary to evaluate disturbance impacts on the coral reef ecosystem as climate change and marine heatwaves are anticipated to continue into the future.

Key Words

Fish assemblage, marine heatwave, coral reef, functional groups, disturbance, community ecology

1 Introduction

The ocean covers 71% of the Earth's surface and has absorbed more than 90% of the excess heat in the climate system since 1970 (IPCC 2019). Marine heatwaves have been defined as a period of extreme warm sea surface temperature that persists for days to months and can extend up to thousands of kilometers (IPCC 2019). Marine heatwaves have direct and indirect implications for coastal communities, including but not limited to species range shifts, local extinctions and fisheries related economic impacts (Hobday et al. 2016). It has been estimated that marine heatwaves have doubled in frequency since 1982 and are increasing in intensity over time (IPCC 2019).

Corals are especially sensitive to thermal stress and can act as sentinels of ecosystem-wide shifts. Most corals live in water temperatures close to their upper thermal limit (Spalding & Brown 2015). Coral polyps respond to prolonged heat stress by ejecting the dinoflagellate endosymbionts (Symbiodiniceae) that live in their tissues and provide a portion of their energy and color. As corals lose their symbionts they appear “pale” or “bleached” and become more vulnerable to environmental threats (Hoegh-Guldberg & Smith 1989). Worldwide bleaching events in the last decades have caused mass coral mortality in many regions (Hoegh-Guldberg 1999, Baird & Marshall 2002, Hughes et al. 2007, 2018a, Spalding & Brown 2015).

Corals begin to bleach when the sea surface temperature is 1 °C above the maximum monthly mean (MMM) temperature; NOAA defines the MMM for the main Hawaiian islands to be 27 °C, with a bleaching threshold at 28 °C (Glynn & D’Croz 1990, Jokiel et al. 2005, NOAA Coral Reef Watch, 2020). When the bleaching threshold is exceeded for significant periods of time, it is measured in degree heating weeks (DHW). When the bleaching threshold is exceeded by 1 °C for one week, the DHW value is 1. When DHW values reach four weeks, substantial bleaching can occur, and upon reaching eight weeks, significant coral mortality is expected (University of Hawai‘i Social Science Research Institute 2017).

Coral reefs provide important ecosystem goods and services such as fisheries, tourism, aesthetic and cultural value (Bellwood et al. 2004). Healthy coral reefs have been estimated to add $477 million annually to the Hawai’i economy through tourism, subsistence, recreational and commercial fisheries (Cesar & van Beukering 2004). Residents and visitors rely on coral reefs in Hawai'i for coastline protection, medicinal properties, research, recreation and educational opportunities (Friedlander et al. 2008). 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 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 will severely impact fisheries, the economy, and way of life in Hawai'i (Van Hooidonk et al. 2016).

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 towards modern day exploitation (Friedlander et al. 2003, Hughes et al. 2003, Abaya et al. 2018). Effective management and protection of coral reefs requires an understanding of how environmental changes influence corals and the organisms associated with them. Resilience-based management uses targeted decision making that reduces local human threats while managing systems and processes that encourage resistance and recovery (Graham et al. 2013). Resilience is the ability to absorb shocks while functioning in the same way, the capacity for recovery following a disturbance, and the degree to which a system can adapt to new conditions (Nyström et al. 2000, Bernhardt & Leslie 2013). This management strategy has increasingly become of interest, as it is a proactive versus reactive approach (Hughes et al. 2007). Better understanding of ecosystem attributes that allow some reefs to be more resilient than others is paramount, especially in anticipation of future climate changes.

In spring of 2014, the first of several marine heatwaves were reported by the US National Oceanic and Atmospheric Administration (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 (Coral Bleaching Recovery Plan 2017). In 2014 and 2015, back-to-back marine heatwaves caused severe coral bleaching and on average, 50% of coral cover loss was estimated along the west coast of the Big Island of Hawai'i, henceforth referred to as "West Hawai'i" (NOAA Coral Reef Watch 2015, Coral Bleaching Recovery Plan 2017).

In this study we analyzed 11 years of subtidal video survey data from an ongoing reef monitoring program in three study areas along West Hawai'i. We examined fish assemblages and used the relative abundance of functional groups (i.e., guilds), and the species driving change within these groups, as indicators for coral health and resilience (Bellwood et al. 2004). Functional groups were determined by a combination of life history characteristics and trophic level (Steneck & Dethier 1994). The seven functional groups consisted of predators, secondary consumers, planktivores, corallivores and three herbivores: scrapers, grazers and browsers.

Herbivorous fish in particular have been identified as an important indicator for coral reef health and resilience (Green & Bellwood 2009). Scrapers such as *Scarus psittacus* are fish that remove algae and sediment by scraping the reef surface. They graze on epilithic algal turf and provide substratum for coral recruitment. Grazers such as *Acanthurus nigrofuscus* and *Zebrasoma flavescens* also graze on the epilithic algal turf, but do not scrape the reef substratum. Browsers such as *Naso lituratus* feed on macroalgae and can play a critical role in reversing coral-algal phase shifts. While these fish play import ecological roles, they are also commonly targeted for subsistence and recreational fishing (Mumby et al. 2007, Highest et al. 2010). Herbivores are a culturally significant food source and play an important role in the island's food security (DAR, 2020). Herbivore management areas have been cited as the highest recommended resilience-based management intervention in Hawai'i to reduce coral reef vulnerability to climate impacts (Graham et al. 2013, Anthony et al. 2015, Chung et al. 2019). Monitoring how herbivore functional group abundance is impacted by disturbances such as marine heatwaves can provide coastal managers additional data to better inform science-based decision making.

The goals of this study were to (1) investigate how fish assemblages were affected by the marine heatwave of 2014 - 15, (2) analyze changes in relative abundance of fish functional groups after the marine heatwave, and (3) identify whether tang species abundance be predicted by environmental variables such as sea surface temperature or coral cover.

2 Materials and Methods

2.1 Study area

The reef sites surveyed were located in West Hawai'i, USA. Surveys were conducted annually in late January or early February, from 2009 - 2019. Survey locations encompass two sites in each of three areas (Mahukona, Puakō, and Old Kona Airport), for a total of six sites (Figure 1). Transect initiation points were marked with Global Positioning System (GPS) locations and unique structures were identified to ensure that each transect started at the same point each year. Each transect of 100 meters ran along a vertical coral or rock face. Because 100 meters of transect tape can be unwieldy underwater, divers would swim 50 meters away from the start point, return, and swim 50 meters away from the start point in the opposite direction to complete the 100 meter long transect. Depth at the start point and at each end of the transect were recorded. Four transects per site were attempted each year, but not always completed if conditions (wave action or visibility) were poor.

All six sites were located within the West Hawai'i Regional Fishery Management Area which spans the entire western coastline of Hawai'i island from Ka Lae, Ka'ū (south point) to 'Upolu Point, North Kohala, from the highwater mark on shore seaward to the limit of the State's management authority (HAR 13-60.4). The administrative rule for this management area was implemented on 31-Dec-1999, amended on 01-Aug-2005 and 26-Dec-2013, and includes some species and gear restrictions. The sites in Mahukona were subject to only these regulations and the sites in Puakō and Kona included additional management designations. Puakō is within a Fish Replenishment Area (FRA), established on 28-Jan-1985 and amended 26-Dec-2013 (HAR 13-54). Old Kona airport is within a Marine Life Conservation District (MLCD), established on 11-Jul-1992 and amended 01-Aug-2005 (HAR 13-37). The prohibited activities in this area are the most extensive. In 2013, a new rule was implemented that only allowed collection of fish 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 put into place across the entire region. See Figure 2 for timeline of Hawai'i Administrative

Rules and Regulations. For the purposes of this study, Mahukona is considered "mostly open", Puakō is "semi-closed" and Kona is "mostly closed" to fishing (See Appendix I for the full list of fishing regulations and regulation map from Hawai'i Division of Aquatic Resources).

The three study areas vary in levels of habitat complexity, oceanographic conditions, urbanization and human population (Table 1). The Mahukona area (sites 6 and 7) is located just over 600 m north of Lapakahi State Park, a Marine Life Conservation District. Mahukona is in a remote location far from populated areas, with a small number of residential homes near the park (<1,000 residents, Census 2016). Puakō (sites 1 and 2) is a small coastal residential community (<1,000 residents, Census 2016), with a large well-developed adjacent coral reef (Hayes et al. 1982), popular for authorized subsistence and recreational fishing, snorkel/dive tourism and luxury shoreline residences (Walsh et al. 2020). Old Kona Airport (sites 3 and 4) is located just north of the large town Kailua-Kona with both residential and commercial occupancy (>13,000 residents, Census 2016).

2.2 Data Collection and Video Transect Analysis

Underwater videos were recorded by trained Seattle Aquarium divers while conducting strip transect surveys. Two scuba divers swam side to side for the length of the 100 m transect, 1 m above the substrate and 1 m from the reef. One diver operated the camera and the other laid out the transect tape and counted and identified all fish within the camera field of view (4 m) using a full-face mask with communication system. 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 quality of video technology increased and became available. 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 divers speaking. Surveys were conducted between 1000 and 1500 hours to standardize quality (light, fish behavior, visibility). The Mahukona sites were not surveyed in 2009 and 2015 due to inability to access the dive sites (sea state and broken ladder).

Videos were analyzed visually for fish diversity and abundance by Seattle Aquarium staff members using commercially available software and high-definition monitors (VLC Media Player, version 3.0.8). Counting teams consisted of two to three staff members with professional expertise in Hawai'i reef fish identification and were from the same group of individuals that conducted the surveys. Fish were counted both on the forward leg of the transect and the reverse leg returning to the start point of the survey. Fish were identified to species (or genus when necessary) and counted.

Coral cover was quantified by taking screenshots of each video and using the open source software CoralNet (coralnet.ucsd.edu, Beijbom et al. 2015). 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. Each point was classified as live coral, dead coral, sand, hard substrate, fish, unknown, water or crustose coralline algae. Fine and fleshy algae were rarely seen and not included in this analysis. Data were averaged per site per year to determine change in percent live and dead coral cover over the study period.

2.3 Sea Surface Temperature Data

Environmental data were downloaded from publicly available datasets 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 reported the marine heatwave beginning in spring 2014 (Walsh et al. 2020). Because our surveys occurred in winter, calendar years 2015 - 2019 were considered post heatwave 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 two groups used in this analysis.

2.5 Data Analyses

All calculations were performed in R (version 4.0.3; R Core Team 2020). Level of significance was set at $\alpha < 0.05$. Fish counts were averaged over the number of transects per site per year and categorized by seven functional groups. Trophic level and life history characteristics were checked against resources to aid in categorization of functional groups (Hobson 1974, Hoover 2008, Donovan et al. 2017, DAR 2014, Coral Reef Network 2005).

Abundance data were non-normally distributed, so non-parametric tests of significance were used. Multivariate non-metric multidimensional scaling (NMDS) techniques were used to visually assess patterns of change in fish assemblage between the three study areas for years before the marine heatwave (2009 - 2014) and years after the marine heatwave (2015 - 2019). 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). An analysis of similarity test (ANOSIM) was used to test the NMDS ordination for significance. Values close to 0 indicate an even distribution of rank within and between sites. Values close to 1 suggest dissimilarity between sites.

Multiple permutational analysis of variance (PERMANOVA) tests were used to examine whether fish assemblage structure was different before and after the heatwave (adonis, vegan package). The three areas were first analyzed collectively, then separately. For each area, PERMANOA tests were performed for total abundance, then individually for each of the seven functional groups.

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).

Species richness, 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. The Shannon-Wiener index is a calculation of diversity in which communities of low diversity have values close to 0. This index is sensitive to species richness, so Simpson diversity was also calculated. The Simpson index uses weighted arithmetic means and is less sensitive to richness. The complement to Simpson's D was calculated (1 - index), in which communities with low diversity have values close to 0, so Shannon and Simpson comparisons could easily be made.

Linear mixed-effects models were used to test for variation in specific species counts against environmental variables within areas (lmer, lmerTest package). Counts of the two most abundant herbivore species across the entire study area, *Z. flavescens* (yellow tang) and *A. nigrofuscus* (lavender tang), were made. Two sets of models were developed. We tested each of the fixed effects, sea surface temperature or percent dead coral cover, with a dummy variable indicating years before or after the marine heatwave with site as a random effect. Models were created for each of the three areas, as follows:

Yellow tang ~ SST * Heatwave (pre/post) + Year + (1|Site)
Yellow tang ~ DeadCoral * Heatwave (pre/post) + Year + (1|Site)
Lavender tang ~ SST * Heatwave (pre/post) + Year + (1|Site)
Lavender tang ~ DeadCoral * Heatwave (pre/post) + Year + (1|Site)

3 Results

3.1 Data Summary

Monthly average sea surface temperature ranged from a minimum of 24.2 °C in March, 2009 to 29.8 °C in September, 2015 (Table 2, Figure 3). Seasonal fluctuations are observed with low average temperatures of 26.1 ± 0.7 °C in the winter months (Dec, Jan, Feb) and high average temperatures of 28.2 ± 0.8 °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 observed in September, 2015. Stations in Kona reported DHW values of 4 and 8 weeks during the back to back marine heatwaves in 2014 and 2015 (University of Hawaiʻi Social Science Research Institute 2017).

Percent dead coral cover ranged from 5.9 to 27.6% (Figure 4). Lowest dead coral cover (5.9 - 15.7%) was observed at Mahukona, followed by Puakō (10.2 - 25.9%) and Kona (16.2 - 27.6%). In all three areas, there was a striking increase in dead coral cover after 2015.

Analysis of the influence of sea surface temperature or percent dead coral cover on two tang species using linear mixed-effects models revealed no statistical significance in any of the predictor variables. These environmental variables (SST and percent dead coral cover) do not seem to be reliable predictors of variation for these tang species.

All fish were counted and identified to species or genus (Table 3). Among the three study areas, individuals from Mahukona made up 11.3% of the dataset (n = 2,428 fish), individuals from Puakō made up 26.8% (n = 5,771 fish), and individuals from Kona made up 62.0% (n = 13,361 fish). The most abundant fish was *Chromis vanderbilti* (blackfin chromis), a planktivorous damselfish, with 12,529 individuals. The most frequently observed fish species was *A. nigrofuscus* (lavender tang), a grazer surgeonfish, present in 99% of transects.

Fish assemblage composition by functional group changed after the marine heatwave in all three study areas (Figure 5). There was a clear shift in the distribution of points between pre- and post-heatwave; this was more evident for Puakō and Kona than Mahukona. Fish assemblages among the three areas were more similar to each other after the heatwave than prior to the heatwave. The visual patterns were statistically supported by the ANOSIM test. We found that fish assemblages differed by area (R = 0.6, sig = 1e-04) and were more similar post heatwave (R = 0.1, sig = 0.04). The PERMANOVA results indicated that area explained 56% of the variance ($R^2 = 0.56$, $p < 0.001$) and period explained 11% ($R^2 = 0.56$, $p < 0.01$).

Diversity indices (Shannon-Wiener, Simpson, and richness) were calculated for all six sites (Figure 7). Shannon-Wiener values ranged from a minimum of 0.18 to a maximum of 1.21, Simpson values ranged from 0.05 to 0.50, and species richness ranged from 30 to 59 across all sites.

3.2 Mahukona

Total abundance of fish in Mahukona ranged from a minimum of 111 total fish counted in 2011 to a maximum of 497 fish in 2016 (Figure 6A). All years surveyed post-marine heatwave showed higher total abundance counts than years prior. The relative abundance of functional groups was significantly different pre- and post-heatwave periods (PERMANOVA Pseudo-$F_{1,7}$ = 4.14, p <0.05) and a dummy variable dividing the data into two groups (pre- and post-heatwave) explained 34% of the variance in the data. Fish assemblage by species was significantly different post-heatwave (PERMANOVA Pseudo-$F_{1,7}$ = 3.65, p <0.05) and the heatwave variable explained 37% of the variance (data not shown). The largest functional groups by abundance were secondary consumers, followed by grazers and planktivores (Figure 6B). These three groups were found to account for 94% of the difference in total fish assemblage post-heatwave. Only species within the grazers (PERMANOVA Pseudo-$F_{1,7}$ = 13.68, p <0.05) and secondary consumers (PERMANOVA Pseudo-$F_{1,7}$ = 2.34, p <0.05) were significantly different post-heatwave. Five fish species accounted for 73% of the difference post-heatwave: *C. vanderbilti* (blackfin chromis), *Z. flavescens* (yellow tang), *A. nigrofuscus* (lavender tang), *Ctenochaetus strigosus* (goldrim kole tang) and *Mulloidichthys flavolineatus* (yellowstripe goatfish).

Diversity index values (Shannon-Wiener and Simpson, respectively) ranged from a minimum of 0.18 and 0.05 in 2011 to a maximum of 0.63 and 0.23 in 2016. Species richness ranged from 30 to 48. Mahukona had the lowest diversity and richness values among the three sites.

3.3 Puakō

Total abundance of fish in Puakō ranged from a minimum of 207 total fish counted in 2009 to a maximum of 982 fish in 2019 (Figure 7A). The relative abundance of functional groups was significantly different pre- and post-heatwave periods (PERMANOVA Pseudo-$F_{1,9}$ = 7.63, p <0.05) and a dummy variable dividing the data into two groups (pre- and post-heatwave) explained 46% of the variance in the data. Fish assemblage by species was also significantly different post-heatwave (PERMANOVA Pseudo-$F_{1,9}$ = 4.82, p <0.05) and the heatwave variable explained 35% of the variance (data not shown).

The largest functional groups by abundance were secondary consumers, followed by grazers and planktivores (Figure 7B). These three groups accounted for 94% of the difference in total fish assemblage post-heatwave. Only species within the grazer functional group were significantly different post-heatwave (PERMANOVA Pseudo-$F_{1,9}$ = 5.74, p <0.05). Six fish species accounted for 71% of the difference post-heatwave: *Chromis agilis* (agile chromis), *Abudefduf adbominalis* (hawaiian sergeant), *Z. flavescens* (yellow tang), *A. nigrofuscus* (lavender tang), *C. strigosus* (goldrim kole tang) and *Melichthys niger* (black trigger).

Diversity index values (Shannon-Wiener and Simpson, respectively) ranged from a minimum of 0.25 and 0.08 in 2009 to a maximum of 1.07 and 0.40 in 2016. Species richness ranged from 30 to 59. The Puakō sites showed the largest increase in diversity and richness values over the study period, indicating more change in the number of total species and rare species in this area compared to the other two areas.

3.3 Kona

Total abundance of fish in Kona ranged from a minimum of 892 total fish counted in 2009 to a maximum of 1,640 fish in 2013 (Figure 8A). The relative abundance of functional groups was significantly different pre- and post-heatwave periods (PERMANOVA Pseudo-$F_{1,9}$ = 10.98, p <0.01) and a dummy variable dividing the data into two groups (pre- and post-heatwave) explained 55% of the variance in the data. Fish assemblage by species was also significantly different post-heatwave (PERMANOVA Pseudo-$F_{1,9}$ = 8.28, p <0.01) and the heatwave variable explained 48% of the variance (data not shown).

The largest functional groups by abundance were planktivores, followed by grazers and secondary consumers (Figure 8B). The two groups planktivores and grazers accounted for 82% of the difference in total fish assemblage post-heatwave. Species diversity within the planktivores (PERMANOVA Pseudo-$F_{1,9}$ = 7.81, p <0.05), grazers (PERMANOVA Pseudo-$F_{1,9}$ = 6.77, p <0.05) and secondary consumers groups (PERMANOVA Pseudo-$F_{1,9}$ = 4.62, p <0.01) were significantly different post-heatwave. Three fish species were identified as driving 72% of the difference post-heatwave: *C. vanderbilti* (blackfin chromis), *Z. flavescens* (yellow tang) and *A. nigrofuscus* (lavender tang).

Diversity index values (Shannon-Wiener and Simpson, respectively) ranged from a minimum of 0.74 and 0.32 in 2009 to a maximum of 1.21 and 0.49 in 2014. Species richness ranged from 35 to 53. The Kona sites showed consistently high diversity values throughout the study period, with less change over time than observed in Puakō (Figure 9).

4 Discussion

In the last 40 years, marine heatwaves have increased in intensity and doubled in frequency due to human-induced climate change (IPCC 2019). These disturbances continue to have large impacts on thermally sensitive coral reef ecosystems (Hughes et al. 2018b). The goals of this research were to (1) investigate how fish assemblages in Hawaii were affected by the marine heatwave of 2014 - 15, (2) analyze changes in relative abundance of fish functional groups after the marine heatwave, and (3) identify whether tang species abundance can be predicted by environmental variables such as sea surface temperature or coral cover.

Our study of coral reef fish assemblages across three areas in West Hawai'i revealed three key findings. First, we found that regardless of habitat differences and management strategies, fish assemblages in these areas became more similar (or more homogeneous), after a major marine heatwave. Second, we found that changes in fish assemblage after the heatwave were driven by the same few species across the study area: *Z. flavescens* (yellow tang), *A. nigrofuscus* (lavender tang), and *C. strigosus* (goldrim or kole tang). There were additional species responsible for changes to specific areas which included *M. flavolineatus* (yellowstripe goatfish) and *C. vanderbilti* (blackfin chromis) in Mahukona, *M. niger* (black trigger), *C. agilis* (agile chromis) and *A. abdominalis* (hawaiian sergeant) in Puakō, and *C.*

vanderbilti (blackfin chromis) in Kona. Third, total fish abundance increased in years after the marine heatwave in the areas with fewer fishing regulations, Mahukona and Puakō, and seemed to remain relatively stable in Kona, the area with higher fishing restrictions.

Fish assemblage was significantly different in the years after the marine heatwave across all three areas. Our findings are similar to a study from Lizard Island, Australia, where overall taxonomic and functional diversity of fish assemblages became more similar across distinct habitat types six months after a bleaching event in 2015 (Richardson et al. 2018). Consistent with our study, these authors found a significant shift towards algae-farming, small-bodied habitat generalist fish. Biotic homogenization has been cited as one of the most pressing global biodiversity crises (Dornelas et al. 2014, Magurran et al. 2015, McGill et al. 2015). Climate change favors generalist consumers, who replace specialist species that cannot adapt to changing environments (Richardson et al. 2018). Increasing numbers of generalist species leads to higher functional similarity and less functional diversity in the community.

The increase in fish abundance seen in our data after the marine heatwave challenges the assumption that coral bleaching leads to net loss of coral dependent reef fish (Wismer et al. 2019). The two areas more open to fishing, Mahukona and Puakō, show increases in fish abundance post marine heatwave, while the area mostly closed to fishing, Kona, remained high throughout the study period. It may be that fish species in this protected area could be closer to carrying capacity than those exposed to higher fishing pressure. The data may also show evidence for habitat shifts, where small bodied grazing fish move into areas with degraded habitat because they do not require live coral to survive (Wismer et al. 2019).

Two environmental variables, sea surface temperature and percent dead coral cover, were not found to be significant predictors for *Z. flavescens* (yellow tang) and *A. nigrofuscus* (lavender tang) abundance. These fish species are highly targeted by the commercial aquarium fishery, likely due to the fact that they can tolerate a range of temperatures making them easy to care for (Bennett 1828). This thermal tolerance may be why the model was not found to be significant. Future work may consider the relationship between sea surface temperature and other species that may be less tolerant to temperature changes. Percent dead coral cover was used as a proxy for substrate availability for filamentous algal growth which tang species feed on. This model was also not significant however, algal cover was not directly measured or included in the model. Future studies may consider investigating this relationship further or exploring fish species that more heavily rely on live coral, such as corallivores. The ability to predict how changing environmental variables impact fish abundances will be helpful for managers to anticipate what changes may occur as climate change continues.

It is important to consider the history and trajectories of change in West Hawai'i to avoid the problem of shifting baselines. Puakō has documented decreases in coral cover and fish abundance over the last 40 years (Minton et al. 2012, Walsh et al. 2018). Studies conducted in 2007 - 2008 found significant decreases in fish abundance compared to references studies in 1978 - 1981 (Hayes et al. 1982). While our study observed increases in total fish abundance over the 11-year study period, these numbers likely do not match historical abundance estimates. These historical observation values were collected with another method and are not comparable to our study results (individuals per m^2 versus per transect). General trends in this historical study were described as the following: 36% decline in piscivores, 46% decline in planktivores, 49% decline in invertivores and 57% decline in herbivores/detritivores. Because it is likely that current abundance estimates are much lower than historical values, additional protective management may be required to rebuild coral and reef fish populations back up to these levels (Walsh et al. 2018).

There are temporal and spatial limitations to this study. The three areas were only surveyed once per year, which does not capture variation that may occur throughout the year (seasonal, etc.). Only fish of a certain size are captured on the camera and can be identified upon viewing the video; juvenile fish and those that utilize the crevices of coral are not recorded. Finally, size and age estimates are not recorded in this study, only presence or absence is documented. Although the study design does have these limitations, the benefits to slowing video and zooming in to identify species is paramount to accurately quantify fish species, especially in areas with high abundances. Additionally, these archived video surveys can be used to help answer future research questions.

Kona, the 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, suggesting ecosystem stability. These sites had the highest diversity values and also documented the highest coral loss. While the fish assemblage was significantly different after the marine heatwave, the observation that fish abundance remained high could indicate this area has higher resilience than the other two areas, and may suggest more stability to new or unusual environmental conditions (Bernhardt & Leslie 2013). Studies have shown that areas with high richness and abundance supporting the same traits (i.e. trait diversity) can withstand environmental disturbance better than those with low redundancy (McLean et al. 2019).

Marine protected areas can be an effective management strategy to prevent overfishing, protect diverse species and provide a refuge for life stages that are more sensitive, but they do not prevent warming of the ocean surface or coral bleaching. However, management policies that prevent overfishing of herbivorous fish, such as browsers or scrapers, can prevent phase shifts from healthy coral reef systems to algal-dominated systems which has been found to aid reef resilience (Hughes et al. 2003). Protected reefs lead to higher diversity indices, allowing for higher trait and functional redundancy in the system to withstand disturbance (McLean et al. 2019). Coral and fish species responses to thermal stress is highly variable, so networks of marine protected areas require thoughtful place-based approaches for effective implementation. Success is dependent on an effective combination of science-based management, public support, and political will (Bellwood et al. 2004). Collaboration and ongoing research and monitoring is necessary to adequately protect and effectively manage Hawai'i's aquatic resources.

5 Conclusions

Despite differences in habitat and management strategy between study areas, three coral reef systems in West Hawai'i exhibited signs of biotic homogenization among fish assemblages following a major marine heatwave event. Changes in fish assemblage over the study period were driven by planktivore, grazer and secondary consumer functional groups. Following the heatwave, fish abundance increased in two areas with low fishing restrictions, while fish abundance in the area with more restrictive fishing regulations remained high and stable. Only a few species appeared to account for major changes in fish abundance, suggesting low functional redundancy in these systems. Continued long term monitoring is important to inform coastal managers as climate change continues to impact the marine environment.

Acknowledgements

This research was funded by the Seattle Aquarium, the Foley Frischkorn Conservation Fund, and the NOAA Coral Reef Conservation Program Domestic Coral Reef Conservation Grant. Special thanks go to the Conservation Programs and Partnerships Team and Life Sciences Team (Tim Carpenter, Andrew Sim, Alan Tomita, Bryan McNeil, Joel Hollander, Jeff Christiansen, Kaela Wuesthoff, Chris VanDamme) for collecting the data and analyzing many video hours. Thanks to the Hawai'i Division of Aquatic Resources for partnering in this project and providing advice and guidance. Thanks to research assistant Jenna Rolf for coral cover analysis. Thanks to the UW Biostatistics department, Zach Randell, Jon Bekker, Eliza Heery, and Brian Tissot for help with multivariate statistics. Thanks to the School of Marine and Environmental Affairs at the University of Washington for the support and guidance through this project.

Literature Cited

Abaya LM, Wiegner TN, Beets JP, Colbert SL, Carlson KM, Kramer KL (2018) Spatial distribution of sewage pollution on a Hawaiian coral reef. Mar Pollut Bull 130:335–347.

Anthony KRN, Marshall PA, Abdulla A, Beeden R, Bergh C, Black R, Eakin CM, Game ET, Gooch M, Graham NAJ, Green A, Heron SF, van Hooidonk R, Knowland C, Mangubhai S, Marshall N, Maynard JA, Mcginnity P, Mcleod E, Mumby PJ, Nyström M, Obura D, Oliver J, Possingham HP, Pressey RL, Rowlands GP, Tamelander J, Wachenfeld D, Wear S (2015) Operationalizing resilience for adaptive coral reef management under global environmental change. Glob Chang Biol 21:48–61.

Baird AH, Marshall PA (2002) Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. Mar Ecol Prog Ser 237:133–141.

Beijbom O, Edmunds PJ, Roelfsema C, Smith J, Kline DI, Neal BP, Dunlap MJ, Moriarty V, Fan TY, Tan CJ, Chan S, Treibitz T, Gamst A, Mitchell BG, Kriegman D (2015) Towards automated annotation of benthic survey images: Variability of human experts and operational modes of automation. PLoS One 10:1–22.

Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. Nature 429:827–833.

Bennett ET (1828) Zebrasoma flavescens. https://www.fishbase.se/summary/6018 (accessed 29 March 2021)

Bernhardt JR, Leslie HM (2013) Resilience to Climate Change in Coastal Marine Ecosystems. Ann Rev Mar Sci 5:371–392.

Cesar HSJ, van Beukering PJH (2004) Economic valuation of the coral reefs of Hawai'i. Pacific Sci 58:231–242.

Chung AE, Wedding LM, Meadows A, Moritsch MM, Donovan MK, Gove J, Hunter C (2019) Prioritizing reef resilience through spatial planning following a mass coral bleaching event. Coral Reefs 38:837–850.

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143.

Coral Reef Network (2005)

http://www.coralreefnetwork.com/marlife/fishes/fishes.htm).

DAR (2014) https://dlnr.hawaii.gov/dar/files/2014/04/fishes_of_hawaii.pdf.

DAR (2020) https://dlnr.hawaii.gov/marine30x30/files/2020/11/2-pager-Importance-of-Herbivores_Aug262020-3.pdf.

Donovan MK, Friedlander A, Donahue M, Jackson J, Toonen R, Oleson K (2017) A Synthesis of Coral Reef Community Structure in Hawaii and the Caribbean

Dornelas M, Gotelli NJ, McGill B, Shimadzu H, Moyes F, Sievers C, Magurran AE (2014) Assemblage time series reveal biodiversity change but not systematic loss. Science (80-) 344:296–299.

Friedlander A, Aeby G, Brown E, Clark A, Coles S, Dollar S, Hunter C, Jokiel P, Smith J, Walsh B, Williams I, Wiltse W (2008) The State of Coral Reef Ecosystems of the Main Hawaiian Islands. state coral reef Ecosyst United States Pacific Free Assoc states:222–269.

Friedlander AM, Brown EK, Jokiel PL, Smith WR, Rodgers KS (2003) Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. Coral Reefs 22:291–305.

Glynn PW, D'Croz L (1990) Experimental evidence for high temperature stress as the cause of El Niño-coincident coral mortality. Coral Reefs 8:181–191.

Graham NA, Bellwood DR, Cinner JE, Hughes TP, Norström A V, Nyström M (2013) Managing resilience to reverse phase shifts in coral reefs. Front Ecol Environ 11:541–548.

Green AL, Bellwood DR (2009) Monitoring Functional Groups of Herbivorous Reef Fishes as Indicators of Coral Reef Resilience - A practical guide for coral reef managers in the Asia Pacific Region. Gland, Switzerland.

Hayes TA, Hourigan TF, Jazwinski SCJ, Johnson SR, Parrish JD, Walsh DJ (1982) The coastal resources, fisheries and fishery ecology of Puakō, West Hawaii.

Hill MO (1973) Diversity and Evenness : A Unifying Notation and Its Consequences Author (s): M . O . Hill Published by : Ecological Society of America DIVERSITY AND EVENNESS : A UNIFYING NOTATION AND ITS CONSEQUENCES '. Ecology 54:427–432.

Hobday AJ, Alexander L V., Perkins SE, Smale DA, Straub SC, Oliver ECJ, Benthuysen JA, Burrows MT, Donat MG, Feng M, Holbrook NJ, Moore PJ, Scannell HA, Sen Gupta A, Wernberg T (2016) A hierarchical approach to defining marine heatwaves. Prog Oceanogr 141:227–238.

Hobson ES (1974) Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish Bull 72:915–1031.

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. Mar Freshw Res 50:839–866.

Hoegh-Guldberg O, Smith GJ (1989) The effect of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals Stylophora pistillata Esper and Seriatopora hystrix Dana. J Exp Mar Bio Ecol 129:279–303.

Van Hooidonk R, Maynard J, Tamelander J, Gove J, Ahmadia G, Raymundo L, Williams G, Heron SF, Planes S (2016) Local-scale projections of coral reef futures and implications of the Paris Agreement. Sci Rep 6:1–8.

Hoover JP (2008) The Ultimate Guide to Hawaiian Reef Fishes. Mutual Publishing, Honolulu, Hawaii.

Hughes T, Jackson J, Kleypas J, Lough J, Marshall P, Palumbi S, Pandolfi J, Rosen B, Roughgarden J (2003) Climate Change, Human Impacts, and the Resilience of Coral Reefs. Science (80-) 301:929–933.

Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison H, Hobbs JPA, Hoey AS, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett M, Schoepf V, Torda G, Wilson SK (2018a) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science (80-) 359:80–83.

Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey AS, Hoogenboom MO, Liu G, McWilliam MJ, Pears RJ, Pratchett MS, Skirving WJ, Stella JS, Torda G (2018b) Global warming transforms coral reef assemblages. Nature 556:492–496.

Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschaniwskyj N, Pratchett MS, Steneck RS, Willis B (2007) Phase Shifts, Herbivory, and the Resilience of Coral Reefs to Climate Change. Curr Biol 17:360–365.

IPCC (2019) The Ocean and Cryosphere in a Changing Climate. A Special Report of the

Intergovernmental Panel on Climate Change. Intergov Panel Clim Chang:1–765.

Kittinger JN, Teneva LT, Koike H, Stamoulis KA, Kittinger DS, Oleson KLL, Conklin E, Gomes M, Wilcox B, Friedlander AM (2015) From reef to table: Social and ecological factors affecting coral reef fisheries, artisanal seafood supply chains, and seafood security. PLoS One 10:1–24.

Magurran AE, Dornelas M, Moyes F, Gotelli NJ, McGill B (2015) Rapid biotic homogenization of marine fish assemblages. Nat Commun 6:2–6.

McGill BJ, Dornelas M, Gotelli NJ, Magurran AE (2015) Fifteen forms of biodiversity trend in the anthropocene. Trends Ecol Evol 30:104–113.

McLean M, Auber A, Graham NAJ, Houk P, Villéger S, Violle C, Thuiller W, Wilson SK, Mouillot D (2019) Trait structure and redundancy determine sensitivity to disturbance in marine fish communities. Glob Chang Biol 25:3424–3437.

NOAA Coral Reef Watch (2015) NOAA Declares Third Ever Global Coral Bleaching Event. http://www.noaanews.noaa.gov/stories2015/100815-noaa-declares-third-ever-global-coral-bleaching-event.html.

NOAA Coral Reef Watch (2020) https://coralreefwatch.noaa.gov/product/5km/tutorial/crw08a_bleaching_threshold.php.

Nyström M, Folke C, Moberg F (2000) Coral reef disturbance and resilience in a human-dominated environment. Tree 15:1–5.

Richardson LE, Graham NAJ, Pratchett MS, Eurich JG, Hoey AS (2018) Mass coral bleaching causes biotic homogenization of reef fish assemblages. Glob Chang Biol 24:3117–3129.

Spalding MD, Brown BE (2015) Warm-water coral reefs and climate change. Sci Mag 350:769–771.

Steneck RS, Dethier MN (1994) A Functional Group Approach to the Structure of Algal-Dominated Communities Author (s): Robert S . Steneck and Megan N . Dethier Published by : Wiley on behalf of Nordic Society Oikos Stable URL : https://www.jstor.org/stable/3545860 REFERENCES Linked r. Oikos 69:476–498.

U.S. Census Bureau (2016) http://records.hawaiicounty.gov/Weblink/1/edoc/95335/Resident Population by Census Designated Places and Districts.pdf (accessed 1 March 2021)

University of Hawaiʻi Social Science Research Institute (2017) Coral Bleaching Recovery Plan.

Walsh WJ, Cotton S, Jackson L, Kramer L, Lamson M, Marcoux S, Martin R, Sanderlin NBS (2020) Findings and Recommendations of Effectiveness of the West Hawai'i Regional Fishery Management Area (WHRFMA).

Walsh WJ, Zamzow JP, Kramer L (2018) Continued long - term decline of the coral reef biota at Puakō and Pauoa , West Hawai'i (1979 – 2008).

Wismer S, Tebbett SB, Streit RP, Bellwood DR (2019) Spatial mismatch in fish and coral loss following 2016 mass coral bleaching. Sci Total Environ 650:1487–1498.

Tables

Table 1: Summary table of characteristics (location, topography, depth, etc.) for each area.

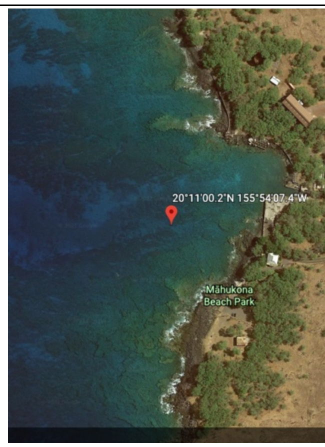
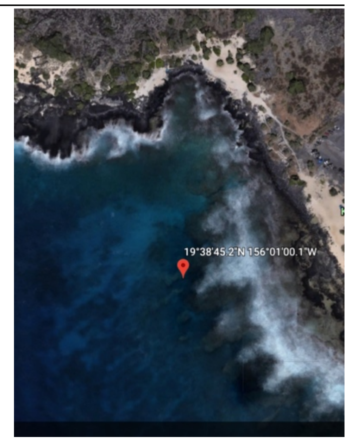
Characteristic	Mahukona	Puakō	Kona
Location	600 meters north of Lapakahi State Park, a Marine Life Conservation District	Offshore of Puakō community	North of Kailua-Kona town
Urban influence	Remote, <1,000 residents (Census, 2016)	Small coastal residential community, <1,000 residents (Census, 2016)	Town with residential and commercial occupancy, >13,000 residents (Census, 2016)
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
Topography			
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

Table 2: Sea Surface Temperature Summary for West Hawai'i from 2009 – 2019.

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 3: Total fish counts and number of species by functional group for each area.

Functional Group (Total species)	Total Fish		Mahukona	Puakō	Kona
Predator (n = 12)	94	Species	8	10	10
		Fish counts	8	58	28
Secondary Consumer (n = 60)	4,935	Species	47	51	40
		Fish counts	991	1,190	1,954
Corallivore (n = 7)	341	Species	7	7	6
		Fish counts	99	126	116
Planktivore (n = 15)	7,256	Species	10	12	7
		Fish counts	575	1,130	5,552
Grazer (n = 14)	8,144	Species	10	12	14
		Fish counts	693	2,174	5,277
Scraper (n = 5)	517	Species	4	5	5
		Fish counts	24	228	266
Browser (n = 5)	272	Species	3	4	5
		Fish counts	39	65	168
Total Count (percent of total)	21,560		2,428 (11.3%)	5,771 (26.8%)	13,361 (62.0%)

Figures

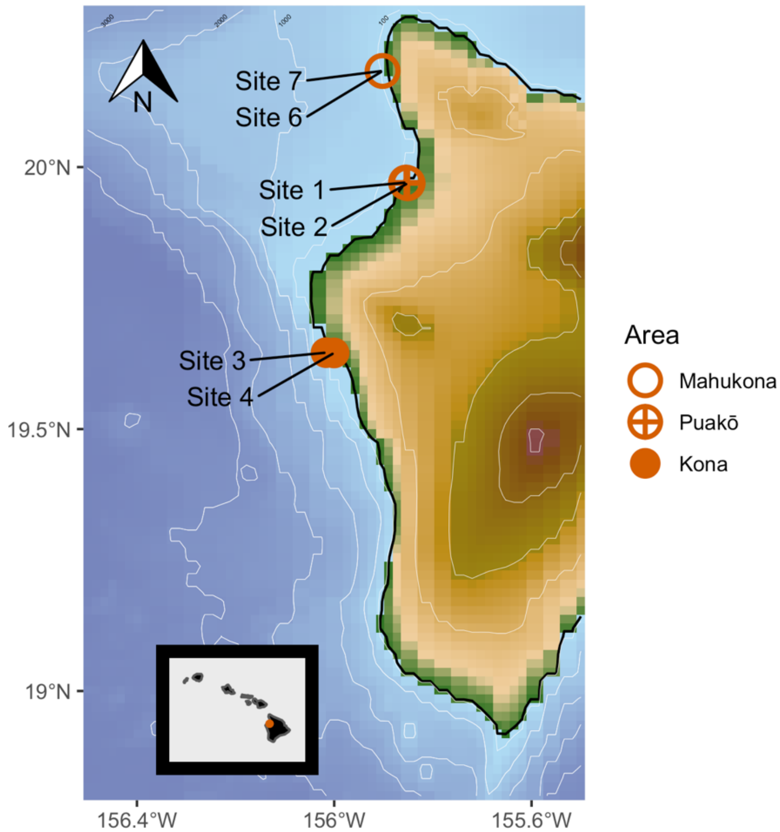


Figure 1: Reef sites surveyed in West Hawai'i (Big Island, USA) from 2009 – 2019. Survey locations encompass two sites (6 and 7) in Mahukona, two sites (1 and 2) in Puakō, and two sites (3 and 4) in Kona. Symbols used for each area represent the level of fishing protection in those areas. Mahukona is 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).

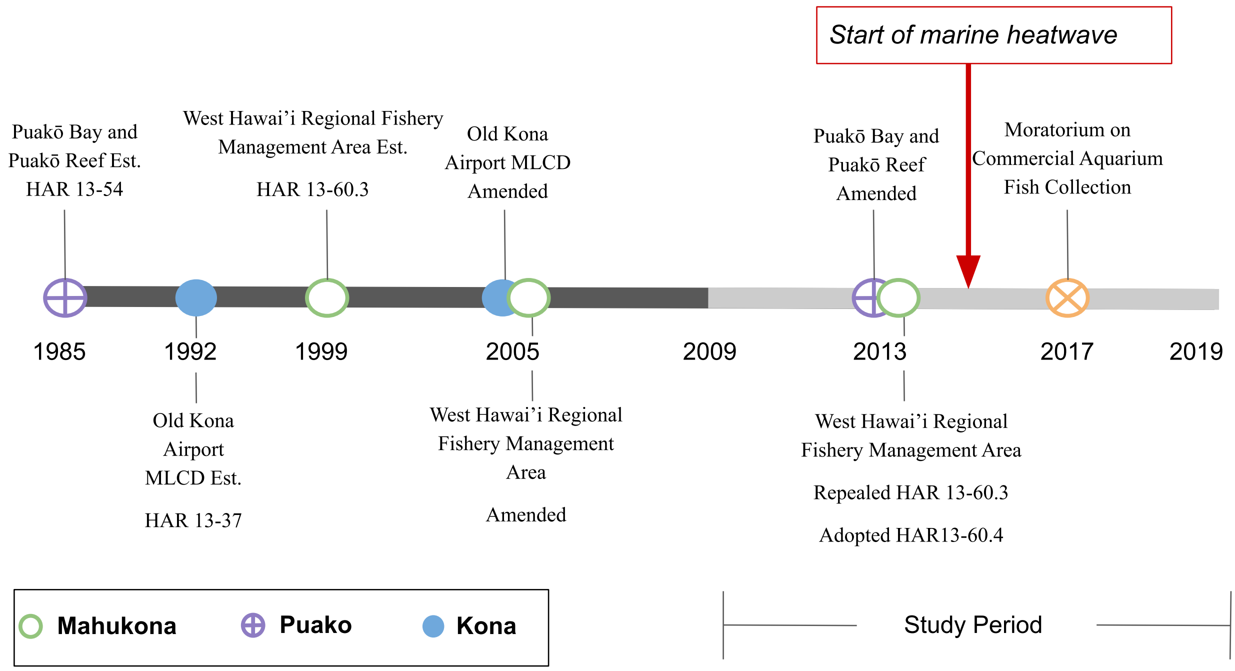


Figure 2: Timeline of Hawai'i Administrative Rules (establishment and amendments) across the three study areas and the onset of the marine heatwave. Symbols used for each area represent the level of fishing protection in those areas. The study period includes 2009 – 2019.

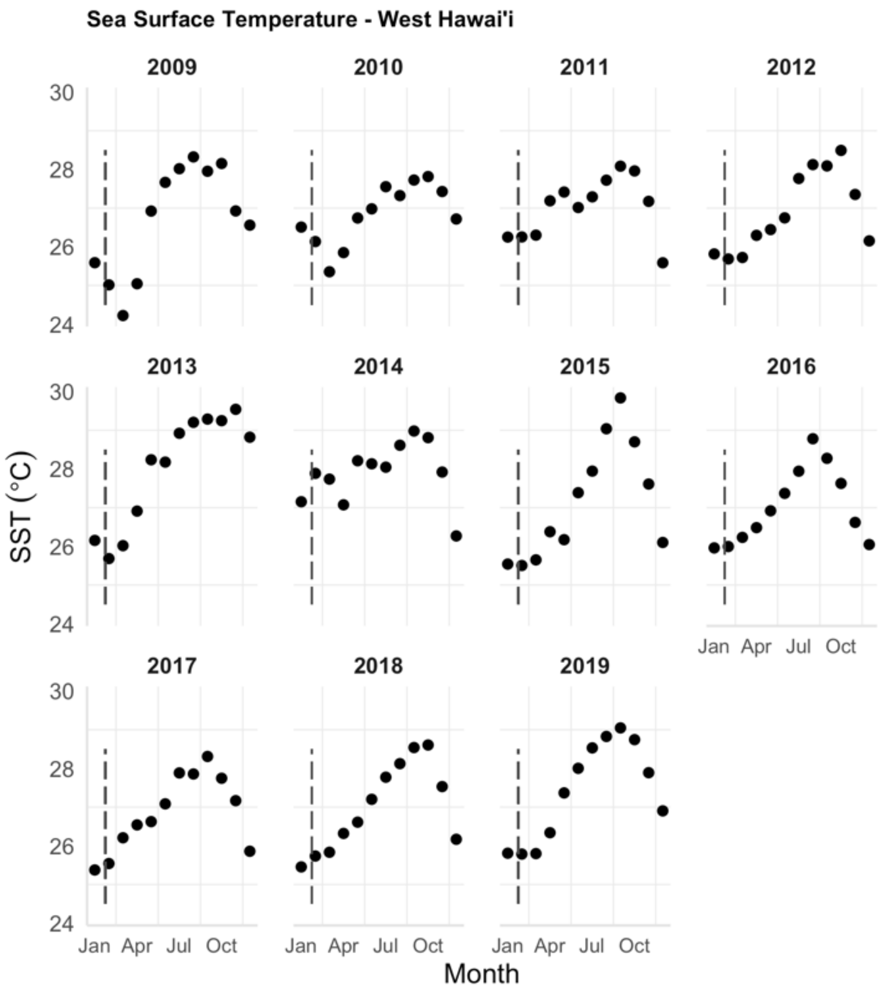


Figure 3: Monthly sea surface temperature (SST, °C) over the study period (2009 - 2019). The marine heatwaves occurred in 2014 and 2015. Peak temperature anomaly occurred in September, 2015.

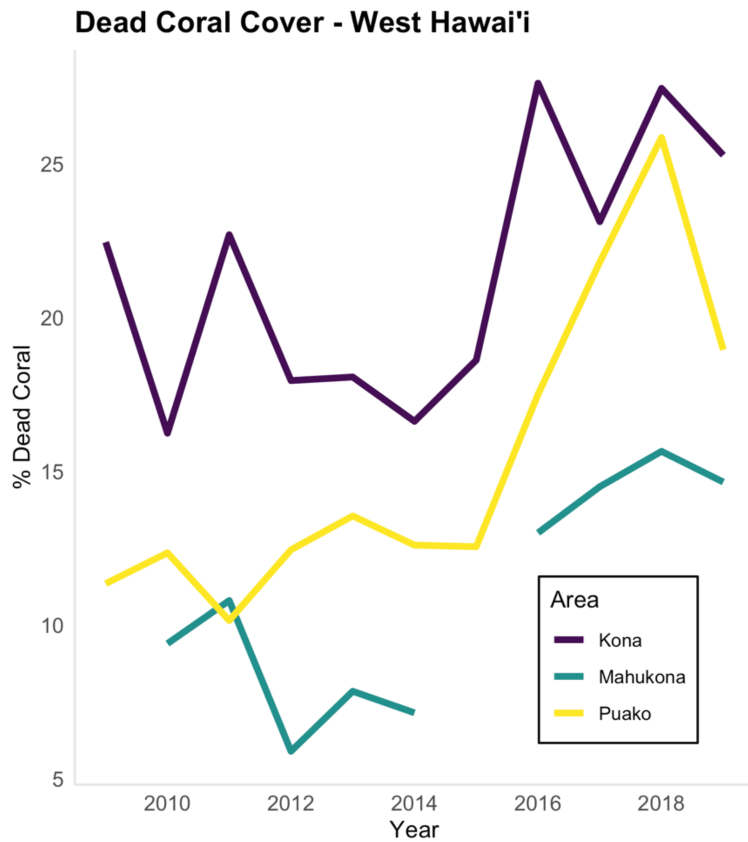


Figure 4: Percent dead coral cover throughout the study period (2009 - 2019) in three areas in West Hawai'i. All three areas increased in dead coral cover post marine heatwave in 2015. Mahukona was not surveyed in 2009 or 2015.

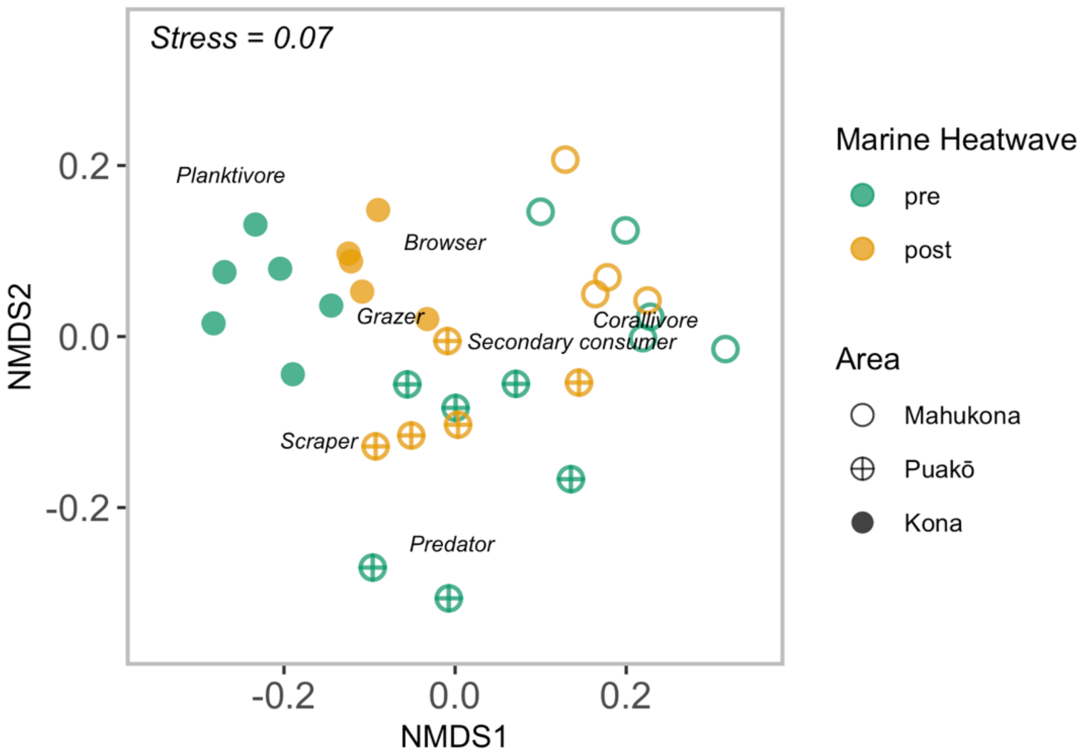


Figure 5: Multivariate non-metric multidimensional scaling (nMDS) techniques were used to assess patterns in changes of fish assemblage before and after marine heatwave (2015) between three areas in West Hawai'i. Ordinations were calculated with Bray-Curtis dissimilarity distance measures. Area symbols designate differences in fishing management. Years before heatwave (green) and after heatwave (orange) showed changes in fish community structure by functional group. The centroid of each functional group is plotted in black text. Fish assemblages across the three areas were more similar to each other after the marine heatwave.

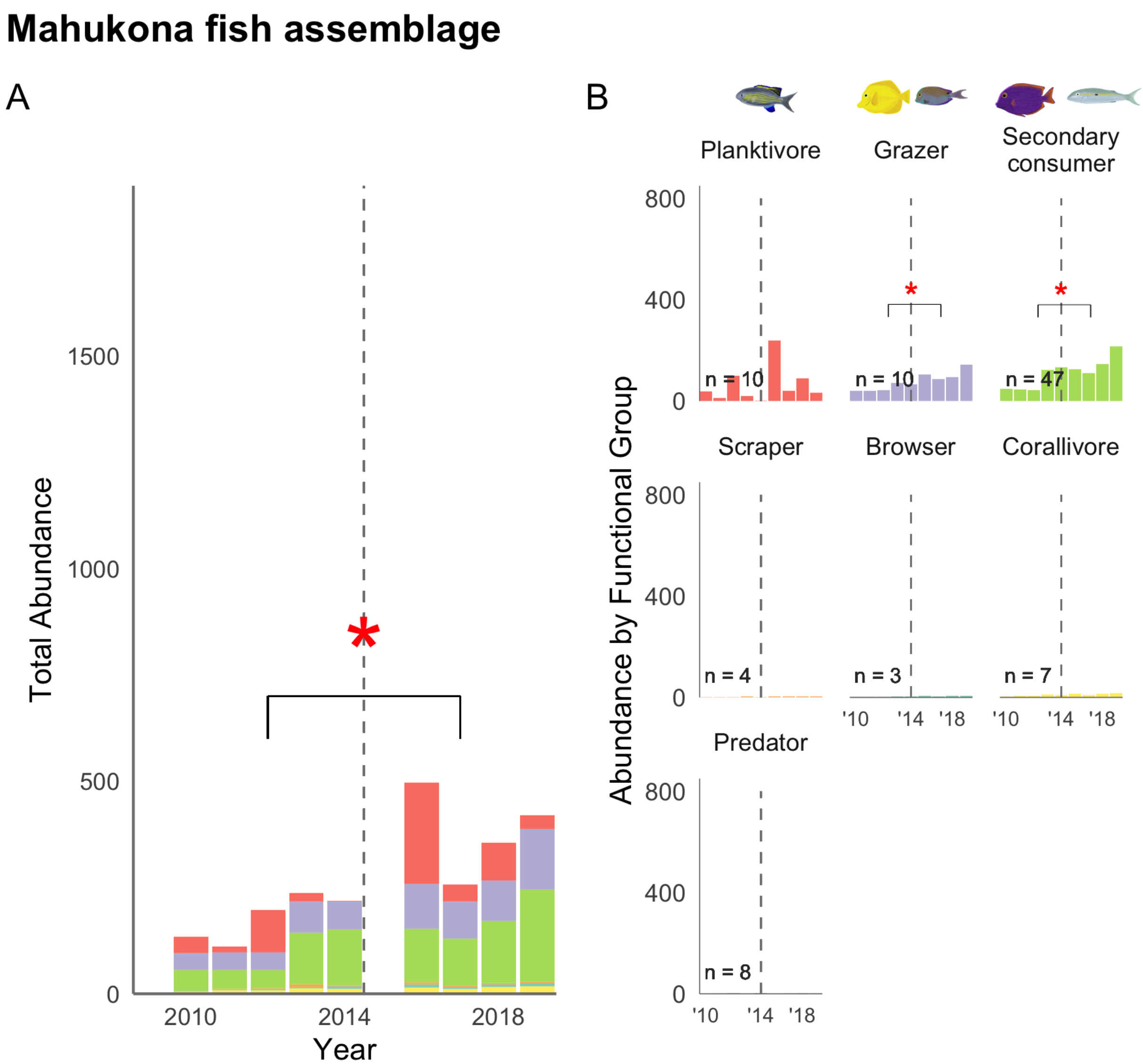


Figure 6: Fish abundance at Mahukona over the study period (2009 – 2019). The vertical dotted line indicates the start of the marine heatwave (2014 - 2015). Red asterisks indicate significant PERMANOVA results of change in fish assemblage after the marine heatwave. (A) Total abundance ranged from 111 fish in 2011 to 497 fish in 2016. Functional groups are identified by colors. (B) Abundance by functional group. The three most abundant functional groups are secondary consumers, grazers and planktivores. The most abundant species within each of these three functional groups are indicated at the top of each histogram. Blackfin chromis (Chromis vanderbilti) in the planktivore category, yellow tang (Zebrasoma flavescens) and lavender tang (Acanthurus nigrofuscus) in the grazer category, goldrim (kole) tang (Ctenochaetus strigosus) and yellowstripe goatfish (Mulloidichthys flavolineatus) in the secondary consumer category. n = number of species within each functional group.

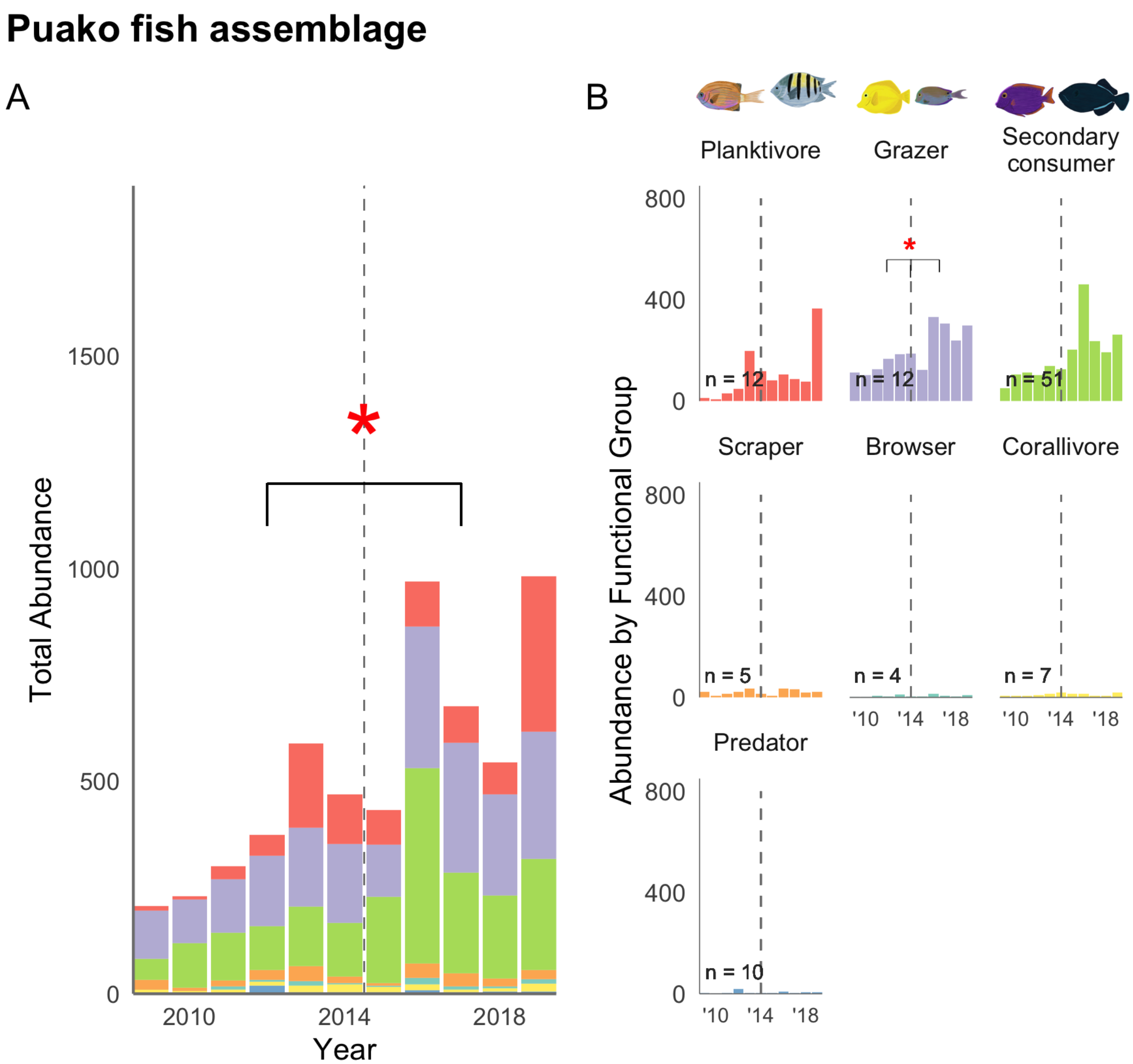


Figure 7: Fish abundance at Puakō over the study period (2009 – 2019). The vertical dotted line designates the start of the marine heatwave (2014 - 2015). Red asterisks indicate significant PERMANOVA results of change in fish assemblage after the marine heatwave. (A) Total abundance ranged from 207 fish in 2009 to 982 fish in 2019. Functional groups are identified by colors. (B) Abundance by functional group. The three most abundant functional groups are secondary consumers, grazers and planktivores. The most abundant species within each of these three functional groups are indicated at the top of each histogram. Agile chromis (Chromis agilis) and hawaiian sergeant (Abudefduf abdominalis) in the planktivore category, yellow tang (Zebrasoma flavescens) and lavender tang (Acanthurus nirofuscus) in the grazer category, goldrim (kole) tang (Ctenochaetus strigosus) and black trigger (Melichthys niger) in the secondary consumer category. n = number of species within each functional group.

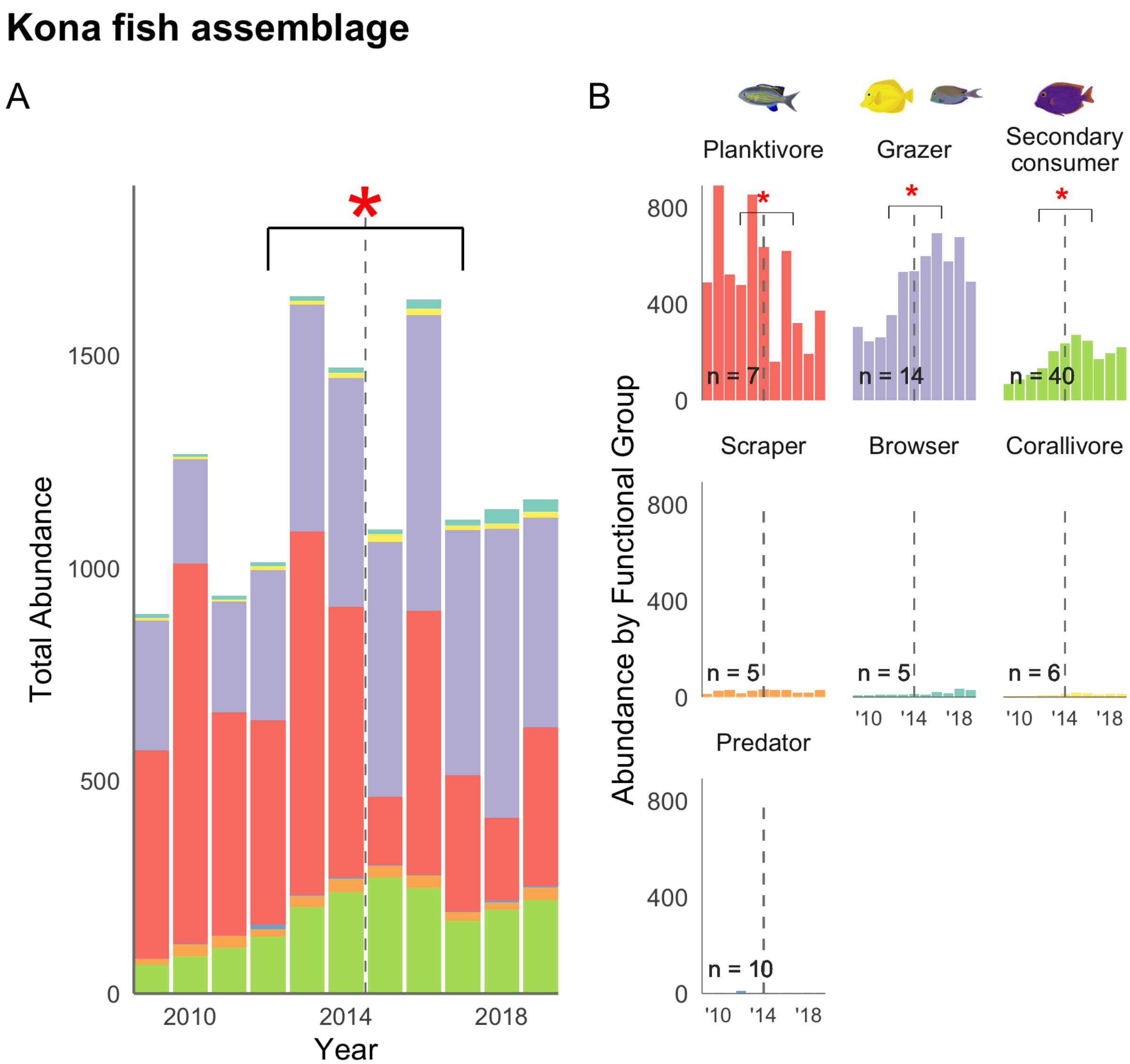


Figure 8: Fish abundance at Kona fish over the study period (2009 – 2019). The vertical dotted line designates the start of the marine heatwave (2014 - 2015). Red asterisks indicate significant PERMANOVA results of change in fish assemblage after the marine heatwave. (A) Total abundance ranged from 892 fish in 2009 to 1,632 fish in 2016. Functional groups are identified by colors. (B) Abundance by functional group. The three most abundant functional groups are planktivores, grazers and secondary consumers. The most abundant species within each of these three functional groups are indicated at the top of each histogram. Blackfin chromis (Chromis vanderbilti) in the planktivore category, yellow tang (Zebrasoma flavescens) and lavender tang (Acanthurus nirofuscus) in the grazer category, goldrim (kole) tang (Ctenochaetus strigosus) in the secondary consumer category. n = number of species within each functional group.

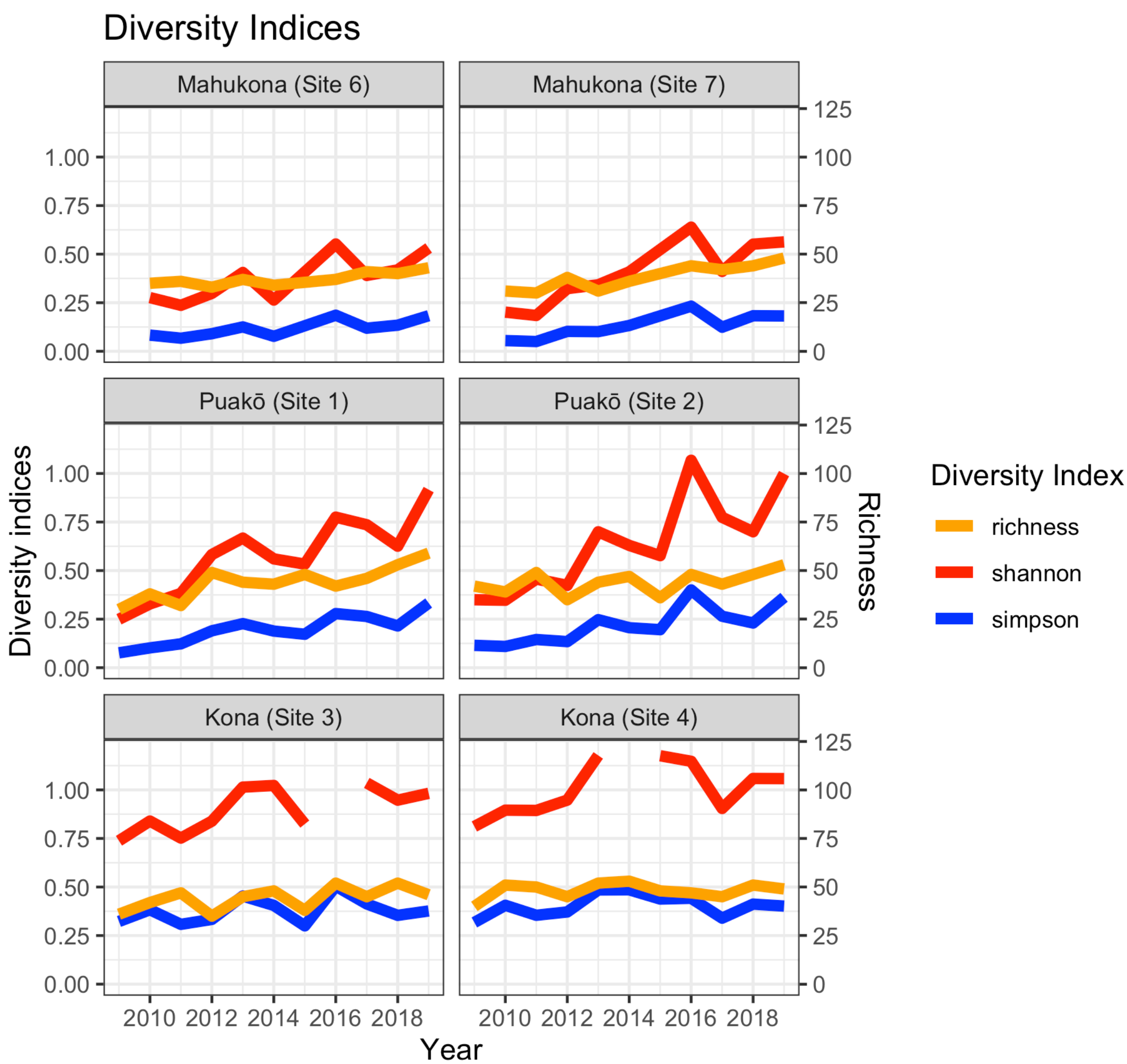
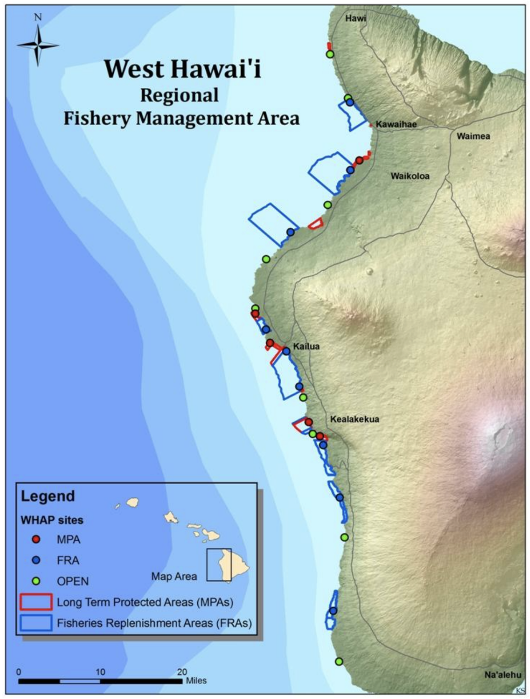


Figure 9: Shannon-Wiener (red), Simpson (blue) diversity indices and species richness (orange) calculations for each pair of sites per area over the study period (2009 - 2019). Mahukona (sites 6 and 7) had the lowest diversity and richness values. Puakō (sites 1 and 2) had the largest increase in diversity and richness values over the study period, indicating more change in the number of total species and rare species in this area compared to other areas. Kona (sites 3 and 4) showed consistently high diversity values throughout the study period, with less change over time than in Puakō.

Appendices

Appendix I: Hawai'i Administrative Rules



Fishery management areas from Hawai'i Division of Aquatic Resources.

Mahukona (and Puakō and Kona)	Puakō	Kona
West Hawai'i Regional Fishery Management Area	Puakō Bay and Puakō Reef	Old Kona Airport Marine Life Conservation District
HAR 13-60.4	HAR 13-54	HAR 13-37
Implemented: 12/31/1999 Amended: 8/1/2005	Established: 1/28/1985 Amended: 12/26/2013	Established: 7/11/1992 Amended: 8/1/2005
Permitted: all types of fishing except as indicated in prohibited activities below	Permitted: To possess aboard any boat or watercraft transiting through the area any legal fishing gear and any fish or other aquatic organism taken outside of the area. With a permit to engage in activities otherwise prohibited by law for scientific, propagation or other purposes.	Permitted: To fish for, take, possess or remove akule by handline at night, and ʻōpelu by lift or ʻōpelu net method using bait or chum for commercial or home consumption. To fish for, take, possess or remove any finfish for home consumption by throw net or pole-and-line (without reel) with bait from shore. To collect wana, wana halula, and hāʻukeʻuke with hand tool, and without use of scuba gear, from June 1 to October 1. To use the state mooring not longer than three hours per boat each day on a first come, first served basis for non-commercial use. Commercial dive/tour operations may be

		conducted at the mooring and from shore with a permit.
Prohibited: To take, kill, possess, sell, or offer for sale, any specimen of the following: Hawaiian stingray, broad stingray, pelagic stingray, spotted eagle ray, blacktip reef shark, gray reef shark, whitetip reef shark, tiger shark, whale shark, horned helmet, and Triton's trumpet. See administrative rule for species list. To possess more than five yellow tang larger than 4.5 inches total length, or more than five yellow tang smaller than 2 inches total length. To engage in SCUBA spearfishing, possess both SCUBA gear and a spear at the same time, or possess SCUBA gear and any specimen of speared aquatic life at the same time. To possess aquarium collecting gear, or take or possess any specimen of aquatic life for aquarium purposes between sunset and sunrise, without a valid aquarium permit or in violation of its conditions, or while on a vessel that does not conform to registration requirements. To possess or use any net or container underwater to capture or hold aquatic life alive for aquarium purposes, which is not labeled with the commercial marine license number(s) of the person(s) owning, possessing, or using the equipment.	Prohibited: To possess or use any type of net except thrownet. To engage or attempt to engage in fish feeding.	Prohibited: To fish for, take, injure, kill, possess or remove any marine life, including live sea shell and 'opihi, live coral, algae or limu, or other marine life, or their eggs, except as indicated in permitted activities above. To take or alter any sand, shell, coral, rock or other geological feature or specimen, or to possess in the water any device that may be used for the taking or altering of marine life, geological feature or specimen. To feed or introduce any food material, substance or device as an attractant, directly to or in the vicinity of any aquatic organism except for the purpose of catching and removing that organism as permitted. To anchor a water craft in the MLCD, or operate a motorboat or other motor powered water craft within the "No Boating Zone" except for emergency or enforcement purposes. To conduct commercial dive/tour activities except as indicated in permitted activities above .

Appendix II: Summary of surveys

Area	Site	Years sampled	Transects
Mahukona	Site 6	2010:2014, 2016:2019	33
	Site 7	2010:2014, 2016:2019	32
Puakō	Site 1	2009:2019	41
	Site 2	2009:2019	39
Kona	Site 3	2009:2019	40
	Site 4	2009:2019	40

Appendix III: Species and functional group list

* aquarium white list (2013)

Scientific name	Common name	Family	Functional group
Abudefduf abdominalis	Hawaiian sergeant	Damselfish	Planktivore
Abudefduf sordidus	Blackspot sergeant	Damselfish	Secondary consumer
Acanthurus guttatus	White spotted surgeonfish	Surgeonfish	Grazer
*Acanthurus achilles**	Achilles tang	Surgeonfish	Grazer
Acanthurus blochii	Ringtail surgeonfish	Surgeonfish	Grazer
*Acanthurus dussumieri**	Eyestripe surgeonfish	Surgeonfish	Grazer
Acanthurus leucopareius	Whitebar surgeonfish	Surgeonfish	Grazer
*Acanthurus nigricans**	Goldrim surgeonfish	Surgeonfish	Grazer
Acanthurus nigroris	Blueline surgeonfish	Surgeonfish	Grazer
*Acanthurus nigrofuscus**	Lavender/brown tang	Surgeonfish	Grazer
*Acanthurus olivaceus**	Orangeshoulder tang	Surgeonfish	Grazer
*Acanthurus thompsoni**	Thompson's surgeonfish	Surgeonfish	Planktivore
Acanthurus triostegus	Convict tang	Surgeonfish	Grazer
Acanthurus xanthopterus	Yellowfin surgeonfish	Surgeonfish	Grazer
Aetobatus ocellatus	Spotted eagle ray	Ray	Secondary consumer
Aluterus scriptus	Scrawled filefish	Filefish	Secondary consumer
Aphareus furca	Forktail snapper	Snapper	Predator
Aprion virescens	Grey snapper	Snapper	Predator
Arothron hispidus	Stripebelly puffer	Puffer	Secondary consumer
Arothron meleagris	Spotted puffer	Puffer	Corallivore
Aulostomus chinensis	Trumpetfish	Trumpetfish	Predator
Bodianus albotaeniatus	Hawai'ian hogfish	Wrasse	Secondary consumer

Calotomus carolinus	Stareye parrotfish	Parrotfish	Browser
Cantherhines dumerilii	Barred filefish	Filefish	Corallivore
Cantherines sandwichiensis	Squaretail filefish	Filefish	Secondary consumer
Canthigaster amboinensis	Ambon toby	Toby	Secondary consumer
Canthigaster coronata	Crown toby	Toby	Secondary consumer
*Canthigaster jactator**	Whitespotted toby	Toby	Secondary consumer
Caranx melampygus	Bluefin trevally	Jack	Predator
Centropyge loriculus	Flame angelfish	Angelfish	Secondary consumer
*Centropyge potteri**	Potter's angelfish	Angelfish	Secondary consumer
*Cephalopholis argus**	Peacock (Roi) grouper	Grouper	Predator
Chaetodon auriga	Threadfin butterflyfish	Butterflyfish	Secondary consumer
Chaetodon ephippium	Saddleback butterflyfish	Butterflyfish	Secondary consumer
Chaetodon fremblii	Bluestripe butterflyfish	Butterflyfish	Secondary consumer
Chaetodon lineolatus	Lined butterfly	Butterflyfish	Secondary consumer
Chaetodon lunula	Raccoon butterflyfish	Butterflyfish	Secondary consumer
Chaetodon lunulatus	Oval butterflyfish	Butterflyfish	Secondary consumer
*Chaetodon miliaris**	Milletseed butterflyfish	Butterflyfish	Planktivore
*Chaetodon multicinctus**	Multiband butterflyfish	Butterflyfish	Corallivore
Chaetodon ornatissimus	Ornate butterflyfish	Butterflyfish	Corallivore
Chaetodon quadrimaculatus	Fourspot butterflyfish	Butterflyfish	Corallivore
Chaetodon reticulatus	Reticulated butterflyfish	Butterflyfish	Secondary consumer
Chaetodon unimaculatus	Teardrop butterflyfish	Butterflyfish	Corallivore
Chlorurus perspicillatus	Spectacled parrotfish	Parrotfish	Scraper
Chlorurus spilurus	Bullethead parrotfish	Parrotfish	Scraper

Chromis agilis	Agile chromis	Damselfish	Planktivore
Chromis hanui	Chocolate dip chromis	Damselfish	Planktivore
Chromis ovalis	Oval chromis	Damselfish	Planktivore
Chromis vanderbilti	Blackfin chromis	Damselfish	Planktivore
Chromis verater	Three spot chromis	Damselfish	Planktivore
*Cirrhilabrus jordani**	Flame wrasse	Wrasse	Secondary consumer
*Coris gaimard**	Yellowtail coris	Wrasse	Secondary consumer
Coris venusta	Elegant coris	Wrasse	Secondary consumer
*Ctenochaetus Hawai'iensis**	Black kole or black surgeonfish	Surgeonfish	Secondary consumer
*Ctenochaetus strigosus**	Kole tang	Surgeonfish	Secondary consumer
*Dascyllus albisella**	Hawai'ian dascyllus	Damselfish	Planktivore
Decapterus macarellus	Mackerel scad	Jack	Planktivore
Diodon holocanthus	Longspine Porcupinefish	Porcupinefish	Secondary consumer
Diodon hystrix	Giant Porcupinefish	Porcupinefish	Secondary consumer
Elagatis bipinnulata	Rainbow runner	Jack	Predator
Fistularia commersonii	Bluespotted cornetfish	Cornetfish	Predator
*Forcipiger flavissimus**	Common longnose butterflyfish	Butterflyfish	Secondary consumer
*Gomphosus varius**	Bird nose wrasse	Wrasse	Secondary consumer
Gymnothorax meleagris	Whitemouth moray	Moray	Predator
*Halichoeres ornatissimus**	Ornate wrasse	Wrasse	Secondary consumer
*Hemitaurichthys polylepis**	Pyramid butterfly	Butterflyfish	Planktivore
Hemitaurichthys thompsoni	Thompson's Butterflyfish	Butterflyfish	Planktivore
Kyphosus spp	Chub or Rudderfish	Chub	Browser
Kyphosus sandwicensis	Gray Chub	Chub	Browser

Labroides phthirophagus	Hawai'ian cleaner wrasse	Wrasse	Secondary consumer
Lutjanus fulvus	Blacktailed snapper	Snapper	Secondary consumer
*Lutjanus kasmira**	Bluestripe snapper	Snapper	Secondary consumer
*Macropharyngodon geoffroy**	Shortnose wrasse	Wrasse	Secondary consumer
Malacanthus brevirostris	Flagtail tilefish	Filefish	Secondary consumer
*Melichthys niger**	Black triggerfish	Triggerfish	Secondary consumer
Melichthys vidua	Pinktail triggerfish	Triggerfish	Secondary consumer
Monotaxis grandoculis	Big eye emperor or Mu	Emperor	Secondary consumer
Mulloidichthys flavolineatus	Yellowstripe goatfish	Goatfish	Secondary consumer
Mulloidichthys vanicolensis	Yellowfin goatfish	Goatfish	Secondary consumer
Myripristis kuntee	Pearly soldierfish	Soldierfish	Planktivore
Myripristis sp.	Soldier fish	Soldierfish	Planktivore
Naso brevirostris	Paletail (Short-Nose) Unicornfish	Surgeonfish	Planktivore
Naso hexacanthus	Sleek unicornfish	Surgeonfish	Planktivore
*Naso lituratus**	Orangespine unicornfish	Surgeonfish	Browser
Naso unicornis	Bluespine unicornfish	Surgeonfish	Browser
Neoniphon aurolineatus	Goldline squirrelfish	Squirrelfish	Secondary consumer
Neoniphon summara	Spot fin squirrelfish	Squirrelfish	Secondary consumer
Novaculichthys taeniourus	Rockmover wrasse	Wrasse	Secondary consumer
*Ostracion meleagris**	Box fish	Boxfish	Secondary consumer
Oxycheilinus unifasciatus	Ringtail wrasse	Wrasse	Predator
Paracirrhites arcatus	Arc-eye hawkfish	Hawkfish	Secondary consumer
*Paracirrhites forsteri**	Blackside (Forsteri) hawkfish	Hawkfish	Secondary consumer
Parupeneus bifasciatus	Doublebar goatfish	Goatfish	Secondary consumer

Parupeneus cyclostomus	Blue goatfish	Goatfish	Secondary consumer
Parupeneus multifasciatus	Manybar goatfish	Goatfish	Secondary consumer
Parupeneus pleurostigma	Sidespot goatfish	Goatfish	Secondary consumer
Pervagor aspricaudus	Yellowtail filefish	Filefish	Secondary consumer
Pervagor spilosoma	Hawai'ian fantail filefish	Filefish	Secondary consumer
Plectroglyphidodon johnstonianus	Blue eyed damsel	Damselfish	Corallivore
Pseudocheilinus evanidus	Disappearing wrasse	Wrasse	Secondary consumer
*Pseudocheilinus octotaenia**	Eightline wrasse	Wrasse	Secondary consumer
Rhinecanthus aculeatus	Lagoon triggerfish	Triggerfish	Secondary consumer
Rhinecanthus rectangulus	Wedgetail triggerfish	Triggerfish	Secondary consumer
Sargocentron sp.	Squirrelfish	Squirrelfish	Secondary consumer
Scarus dubius	Regal parrotfish	Parrotfish	Scraper
Scarus psittacus	Palenose parrotfish	Parrotfish	Scraper
Scarus rubroviolaceus	Ember (Redlip) parrotfish	Parrotfish	Scraper
Seriola dumerili	Amber jack	Jack	Predator
Stegastes marginatus	Hawai'ian (Pacific) gregory	Damselfish	Grazer
Stethojulis balteata	Belted wrasse	Wrasse	Secondary consumer
Sufflamen fraenatus	Bridled triggerfish	Triggerfish	Secondary consumer
Sufflamen bursa *	Lei triggerfish	Triggerfish	Secondary consumer
Synodus sp.	Lizardfish	Lizardfish	Predator
*Thalassoma duperrey**	Saddle wrasse	Wrasse	Secondary consumer
Thalassoma purpureum	Surge wrasse	Wrasse	Secondary consumer
Triaenodon obesus	Whitetip reef shark	Shark	Predator
Zanclus cornutus	Moorish Idol	Moorish Idol	Secondary consumer

*Zebrasoma flavescens**	Yellow tang	Surgeonfish	Grazer
Zebrasoma veliferum	Sailfin tang	Surgeonfish	Grazer