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Temporal patterns in coral reef fish assemblages with varying disturbance levels: A tale of two National Parks in Hawai'i

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Long-term ecological monitoring of coral reefs can reveal the state of the reef communities and responses of different reef components to various pulse and press disturbance events. Here, we describe long-term monitoring of reef fish assemblages from two U.S. National Parks in Hawai'i, Kaloko-Honokōhau National Historical Park (KAHO) and Kalaupapa National Historical Park (KALA) over the past decade. These two parks experience different anthropogenic disturbances as KAHO is highly accessible with multiple types of adjacent land use while KALA is relatively inaccessible, surrounded by large expanses of native forest, and known for having the highest documented fish biomass within the main Hawaiian Islands. The fish assemblages in KAHO were numerically dominated by small-bodied damselfish *Chromis* spp. and herbivorous surgeonfishes *Acanthurus nigrofuscus*, *Ctenochaetus strigosus* and *Zebrasoma flavescens*, while those in KALA were numerically dominated by *Chromis vanderbilti*, *A. nigrofuscus*, *Thalassoma duperrey* and *Paracirrhites arcatus*. Multivariate control charts detected anomalies in the fish assemblages in some years. In KAHO, gradual shifts in the assemblages were detected in recent years due to changes (both increases and decreases) in relative abundances of numerically dominant species including *Chromis agilis*, *C. vanderbilti*, *A. nigrofuscus*, *C. strigosus* and *Z. flavescens*. There was a documented reduction in live coral cover in KAHO due to a bleaching event in 2015, and potential delayed effects of the coral mortality on the fish assemblages were found particularly in the North and South regions of the park. In KALA, increases in the abundances of *Acanthurus* (*A. blochii*, *A. leucopareius*, *A. nigrofuscus*, *A. thompsoni* and *A. triostegus*) and *C. strigosus* were found in 2014, likely due to a large recruitment event that had not been well reported. As localized thermal stress events were detected in both KAHO and KALA in 2019, continuous monitoring of these two parks is critical to assess

how the coral-reef ecosystems under two different human-use scenarios respond to repeated heating events and whether there are immediate as well as delayed effects on reef organisms resulting from losses of live coral tissue and a subsequent decrease in structural complexity provided by the coral.

KEYWORDS

coral reef, fish, multivariate control chart, Kaloko-Honokōhau National Historical Park, Kalaupapa National Historical Park, long-term ecological monitoring, coral bleaching

Introduction

Coral reefs worldwide have been under increasing levels of stress due to warming ocean temperatures and changes in ocean chemistry (Hoegh-Guldberg et al., 2007; Hughes et al., 2018). Thermal stress coupled with increases in the intensity and frequency of extreme weather events, such as storms and flooding, can lead to coral bleaching and subsequent mortality (Loya et al., 2001; Couch et al., 2017) or physical destruction of coral reefs (Woodley et al., 1981; Pascoe et al., 2021). In addition to these “pulse” disturbances, long-term continuous “press” disturbances including nutrient input, contaminants, and sedimentation from adjacent land use, as well as decreases in herbivorous fishes due to unsustainable fishing practices, can gradually alter the state of coral reefs (Brown et al., 1990; Done, 1992; Hunter et al., 1995; Bellwood et al., 2004).

Benthic habitats of coral reefs affect distributions and abundances of reef fishes (Graham and Nash, 2013; Fukunaga et al., 2020). Structural complexity of coral provides three-dimensional structure for reef organisms, and reductions in live coral cover can result in decreases in fish abundance and diversity (Komyakova et al., 2013). Reef fishes can also be influenced by their prey availability, and decreases in corallivorous fish abundance have been reported following mass coral mortality due to coral bleaching (Magel et al., 2020) and *Acanthaster* outbreaks (Kayal et al., 2012). Press disturbances can also have direct and/or indirect negative impacts on abundances of reef fishes (DeMartini et al., 2013; Foo et al., 2021). Ecological monitoring of coral reefs that can capture changes in coral-reef communities resulting from both pulse and press disturbances are, therefore, critical in coral-reef management and allow resource managers to respond to changes with different options.

Coral reef species diversity in the Hawaiian archipelago is relatively low compared to species diversity in the Indo-West Pacific Ocean due to geographic isolation (Grigg, 1983). The

isolation, however, also results in relatively high levels of endemism of reef fishes (Friedlander et al., 2003; Grigg et al., 2008). This makes fish assemblages on Hawaiian coral reefs unique and valuable. The U.S. National Park Service (NPS) manages two park areas encompassing coral reefs in the state of Hawai'i: Kaloko-Honokōhau National Historical Park (KAHO) located on the west side of the island of Hawai'i and Kalaupapa National Historical Park (KALA) located on the north shore of the island of Moloka'i (Figure 1). The spatial extent of the marine area enclosed by the park boundaries is 2.4 km² for KAHO and 8.1 km² for KALA. The reefs inside each park consist primarily of coral colonies on basalt boulder habitat, however KAHO has interspersed aggregated reef structures while KALA has only isolated coral colonies (Brown et al., 2016). Each park supports diverse coral-reef communities as well as endangered/threatened marine organisms including sea turtles and Hawaiian monk seals (Brown et al., 2016).

Of the two parks, KAHO is located approximately 5 km north of Kailua-Kona where the highest human population density and runoff associated with impervious surfaces occur along the coastline of West Hawai'i and approximately one million domestic and international tourists arrive every year (Gove et al., 2019). KAHO is more accessible and has substantially more visitors and users of their marine resource than KALA, including fishers targeting regulated species using permitted fishing gear. In addition to these press disturbances, coral reefs in KAHO were impacted by the global-scale coral bleaching event in 2014 - 2017, during which some coral reefs in Hawai'i exhibited mass bleaching in 2014 and 2015 (Williams et al., 2016; Couch et al., 2017; Eakin et al., 2019). In KAHO, 77% of coral colonies experienced bleaching in 2015 that resulted in a reduction in the mean live coral cover from 33% to 12% (McCutcheon and McKenna, 2021).

In contrast, KALA is isolated geographically by 500-meter cliffs abutting the ocean and surrounding forest with only a foot trail leading into the peninsula. Human access is strictly limited by a permit system according to Hawai'i state law. Access by

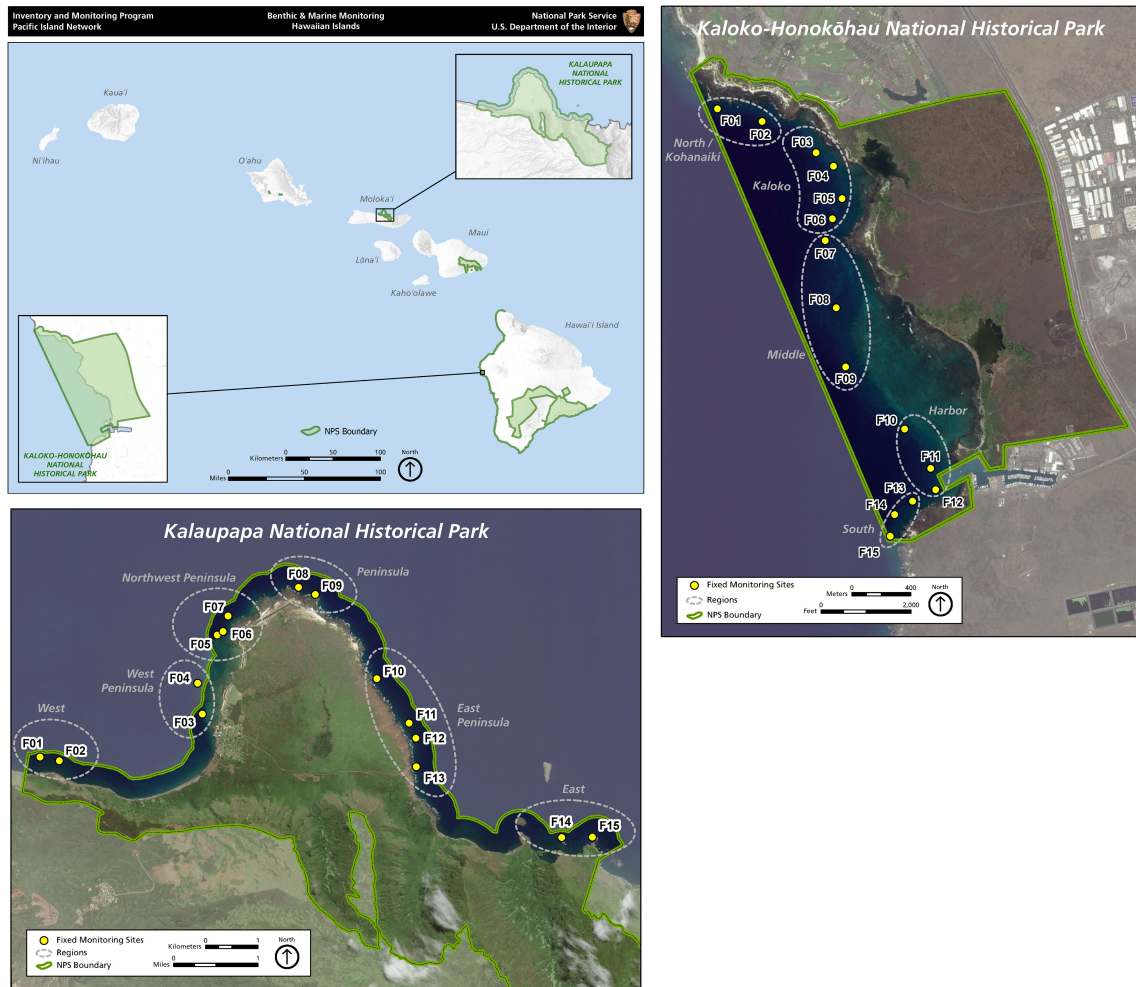


FIGURE 1
Map of the main Hawaiian Islands, showing the locations of the two national parks and permanent survey sites within each park.

boat within the quarter-mile offshore park boundary also requires a permit and is limited seasonally due to high wave events. Threats to coral reefs in KALA due to direct human activities are thus limited, particularly in comparison to those in KAHO. Fishing pressure in KALA is also minimal (Brown et al., 2022), and this location has the highest documented fish biomass in the main Hawaiian Islands (Friedlander et al., 2019), although fish assemblages in the main Hawaiian Islands are overall in a degraded state compared to those in the Northwestern Hawaiian Islands that are largely uninhabited (Friedlander et al., 2018). In addition, coral colonies in KALA experienced little to no bleaching during the 2014 - 2017 global-scale coral bleaching event, maintaining the mean live coral cover of approximately 10% (McCutcheon and McKenna, 2021). Although a localized thermal stress event in 2019 caused 23% of

the colonies to bleach, no significant coral mortality was observed (McCutcheon and McKenna, 2021).

Here we utilized long-term annual reef monitoring data collected by the NPS Pacific Island Inventory and Monitoring Network (PACN) and investigated temporal changes in numerical abundance of reef fish assemblages in the two national parks in Hawai'i (i.e., KAHO and KALA). We hypothesized that the fish assemblages in KAHO would show shifts in the assemblage structure due to the bleaching, as well as existing press disturbances, while those in KALA would be stable. We employed distance-based multivariate control charts (MCCs) to analyze the repeated observations within each park, as this approach allows for investigation of natural temporal variability in a biological community at each site without the need for a site of comparison (e.g., a "control" site

in the Before-After-Control-Impact design) and to identify observations outside of the natural variability (Anderson and Thompson, 2004). We then investigated individual species if MCCs identified any observations outside the natural variability (i.e., anomalous years). The present study offers baseline information about the fish assemblages in the two national parks and how their species compositions have changed over time in recent years. These data provide valuable insights into how disturbance events may alter reef habitats and subsequently impact fish assemblages.

Materials and methods

Survey design

Underwater surveys in KAHO and KALA are conducted annually through the NPS PACN that implements co-located fish and benthic surveys using the marine fish protocol (Brown et al., 2011a) and benthic marine community protocol (Brown et al., 2011b) along 30 (15 fixed/permanent plus 15 temporary/rotational) transects at survey sites ranging from 10 to 20 m in depth. The present study focused on fish data from the 15 fixed/permanent transects from each park to utilize the repeated observations and examine site-specific temporal changes in the fish assemblages.

Fish surveys were conducted during summer months from 2007 to 2011 and from 2014 to 2019 at 15 fixed monitoring sites in KAHO and from 2006 to 2019 at 15 fixed sites in KALA. No fish surveys were conducted in KAHO in 2012 and 2013 due to staffing shortages. For each park, permanent survey sites were numbered and grouped based on geographical proximity as well

as habitat characteristics that reflected the similarity of overall environmental conditions at the sites (Figure 1). For KAHO, the 15 sites were grouped into five regions based on geographic location and benthic composition: North (01 and 02), Kaloko (03, 04, 05 and 06), Middle (07, 08 and 09), Harbor (10, 11 and 12) and South (13, 14 and 15). The Kaloko and Harbor regions have relatively high live coral cover (mostly *Porites* corals) whereas the North, Middle and South regions are basaltic pavement/boulder habitats with relatively high abundance of *Pocillopora meandrina* colonies at the sites 01 and 15 (Table 1). For KALA, the 15 sites were grouped into six regions based on geographic location and wave exposure: West (01 and 02), West Peninsula (03 and 04), Northwest Peninsula (05, 06 and 07), Peninsula (08 and 09), East Peninsula (10, 11, 12 and 13) and East (14 and 15). Sites 01-07 experience winter northwest swells but are shielded from northeast trade-wind swell by the peninsula. Sites 10-15 are primarily impacted by northeast trade wind swell with a secondary impact from dampened northwest winter storm swell. Sites 08 and 09 experience both swell types and subjected to the largest waves. Habitat types of the KALA survey sites are basaltic rock/boulder except for the sites 05 and 06, which are basaltic pavement (Table 1). Isolated colonies of *P. meandrina* are present in the Northwest Peninsula and Peninsula regions except for the site 06 (Table 1). At each survey site, divers who were formally trained for fish identification and survey methods in Hawaiian waters laid a 25-m transect tape parallel to the reef crest along a constant depth contour, enumerated all fishes within 2.5 m on either side of the transect tape (5-m belt) to the lowest possible taxonomic level and visually estimated sizes of all individuals (Brown et al., 2011a).

TABLE 1 Grouping and water depths of KAHO and KALA permanent survey sites.

Region	Permanent site (depth)	Habitat type
KAHO		
North	01 (12.4 m) 02 (19.2 m)	pavement/boulder with <i>Pocillopora meandrina</i> colonies pavement/boulder
Kaloko	03 (11.0 m), 04 (10.5 m), 05 (14.2 m), 06 (13.1 m)	relatively high cover of <i>Porites</i> (<i>P. lobata</i>)
Middle	07 (14.3 m), 08 (14.7 m), 09 (16.3 m)	pavement/boulder
Harbor	10 (13.3 m), 11 (14.8 m), 12 (11.9 m)	relatively high cover of <i>Porites</i> (<i>P. lobata</i> & <i>P. compressa</i>)
South	13 (14.5 m), 14 (14.9 m) and 15 (10.2 m)	pavement/boulder pavement/boulder with <i>Pocillopora meandrina</i> colonies
KALA		
West	01 (17.5 m), 02 (12.9 m)	basaltic rock/boulder
West Peninsula	03 (14.2 m), 04 (18.5 m)	basaltic rock/boulder
Northwest Peninsula	05 (11.2 m), 06 (12.7 m), 07 (20.9 m)	basaltic pavement with <i>Pocillopora meandrina</i> colonies basaltic pavement basaltic rock/boulder with <i>Pocillopora meandrina</i> colonies
Peninsula	08 (15.0 m), 09 (15.9 m)	basaltic rock/boulder with <i>Pocillopora meandrina</i> colonies
East Peninsula	10 (16.3 m), 11 (15.3 m), 12 (17.3 m), 13 (13.6 m)	basaltic rock/boulder
East	14 (14.3 m), 15 (13.7 m)	basaltic rock/boulder

Data analysis

To focus on reef fishes, transient pelagic and semi-pelagic fishes, including the families Carangidae, Belonidae (single observation in the KAHO dataset), Carcharhinidae, Ginglymostomatidae, Dasyatidae and Myliobatidae, were excluded from the analysis. We also focused on numerical abundance of fishes instead of biomass to evaluate the structure of fish assemblages holistically by giving an equal weight to each individual regardless of their size (i.e., avoiding analysis based on biomass that would give larger individuals more weights). Species that did not account for at least 3% of the total fish numerical abundance at a site in any of the surveys were also excluded as interpreting changes in the abundances of rare species is not practical. The 3% cutoff was chosen because it retained approximately 97% of individual reef fish recorded in the study while reducing the number of taxa to approximately half for analysis (see Results for details). The fish assemblage structure was then calculated from the reduced dataset on the basis of the Bray-Curtis dissimilarity after square-root transformation of the fish counts (Clarke, 1993) and used for analyses of fish assemblages over time.

Data from the two parks were analyzed and presented separately due to differences in disturbance levels, disturbance history and environmental conditions. Specifically, we focused on analyzing temporal patterns in the fish assemblages within each park, rather than directly comparing the structures of the fish assemblages between the two parks. Distance-based multivariate control charts (MCCs) were constructed for each region within a park using the vegan package (Oksanen et al., 2022) and custom R scripts in the statistical software R version 4.0.3 (R Core Team, 2020). MCCs are plots of two distances (d_t and d_t^b) calculated in multivariate space based on any distance or dissimilarity measure (Anderson and Thompson, 2004). The distance d_t is the distance/dissimilarity between the observation at time t and the centroid of all observations prior to the time t at a given site, while the distance d_t^b is the distance/dissimilarity between the observation at time t and the centroid of observations designated as a baseline (see Eqs. 4-7 in Anderson and Thompson, 2004 for the equations to calculate d_t and d_t^b). Here, we constructed MCCs for each region within a park to focus on overall temporal trends rather than details at each of the 15 sites. We first obtained the centroid of survey sites within each region for each time point in the space of the Bray-Curtis dissimilarity and used these centroids to calculate d_t and d_t^b . For d_t^b , the first two years of data (i.e., 2007 and 2008 for KAHO and 2006 and 2007 for KALA) were designated as a baseline to test for changes in the fish assemblages since the beginning of the monitoring. Bootstrapping techniques were used to obtain 50% and 95% confidence bounds for both d_t and

d_t^b based on resampling of 1000 times. The 50% confidence bound (i.e., median) is a good representation of the temporal trend in the data. The 95% confidence bound was used as an upper confidence limit under which the status of a given region within each park was considered stable or within natural variability.

We utilized similarity percentage analysis (SIMPER: Clarke and Warwick, 2001) in the software package PRIMER 7 (Clarke and Gorley, 2015) if MCCs indicated changes in fish assemblages that were considered outside natural variability. SIMPER within-group similarity analysis was first used to identify fish taxa that were consistently present in high abundance in each region in “typical” years based on MCCs. SIMPER between-group dissimilarity analysis was then used to identify taxa that contributed to the differences in fish assemblages in the potentially anomalous years as identified by MCCs. Anomalies in fish assemblage structure were considered in comparison to either all previous years or the baseline years based on the results of MCCs.

Results

KAHO

Over the 11 years, 35,447 individuals of reef fishes belonging to 126 taxonomic groups (123 species and 3 groups identified to genus), excluding pelagic and semi-pelagic species, were identified and enumerated along the 15 fixed transects. More than half of these taxonomic groups did not account for 3% or more of fish abundance in any surveys, so excluding less-common species resulted in 34,247 individuals belonging to 52 species for analysis. For all regions (i.e., North, Kaloko, Middle, Harbor and South), the mean numbers of species and fish counts were relatively stable and did not visually show any obvious decreasing or increasing trends (Figure 2).

MCCs detected shifts in the structure of KAHO fish assemblages in recent years on the basis of the Bray-Curtis measure. The shift was mostly gradual and often only detected by d_t^b (distance to the baseline) values and not d_t (distance to all previous years) values (Figure 3). For the North, Middle and South regions, the shifts occurred in the last two years of the study (i.e., 2018 and/or 2019), while d_t^b values identified potentially anomalous years in the Harbor region in 2016 and 2018. In Kaloko, an overall shift in the fish assemblage was detected in 2014, with changes in the assemblages exceeding the d_t^b upper confidence limit in 2015, 2017 and 2018. The exact timing of the shift in the Kaloko region was, however, difficult to determine due to the lack of surveys in 2012 and 2013. Visualization of the assemblage structure based on the Bray-Curtis measure using principal coordinate analysis also

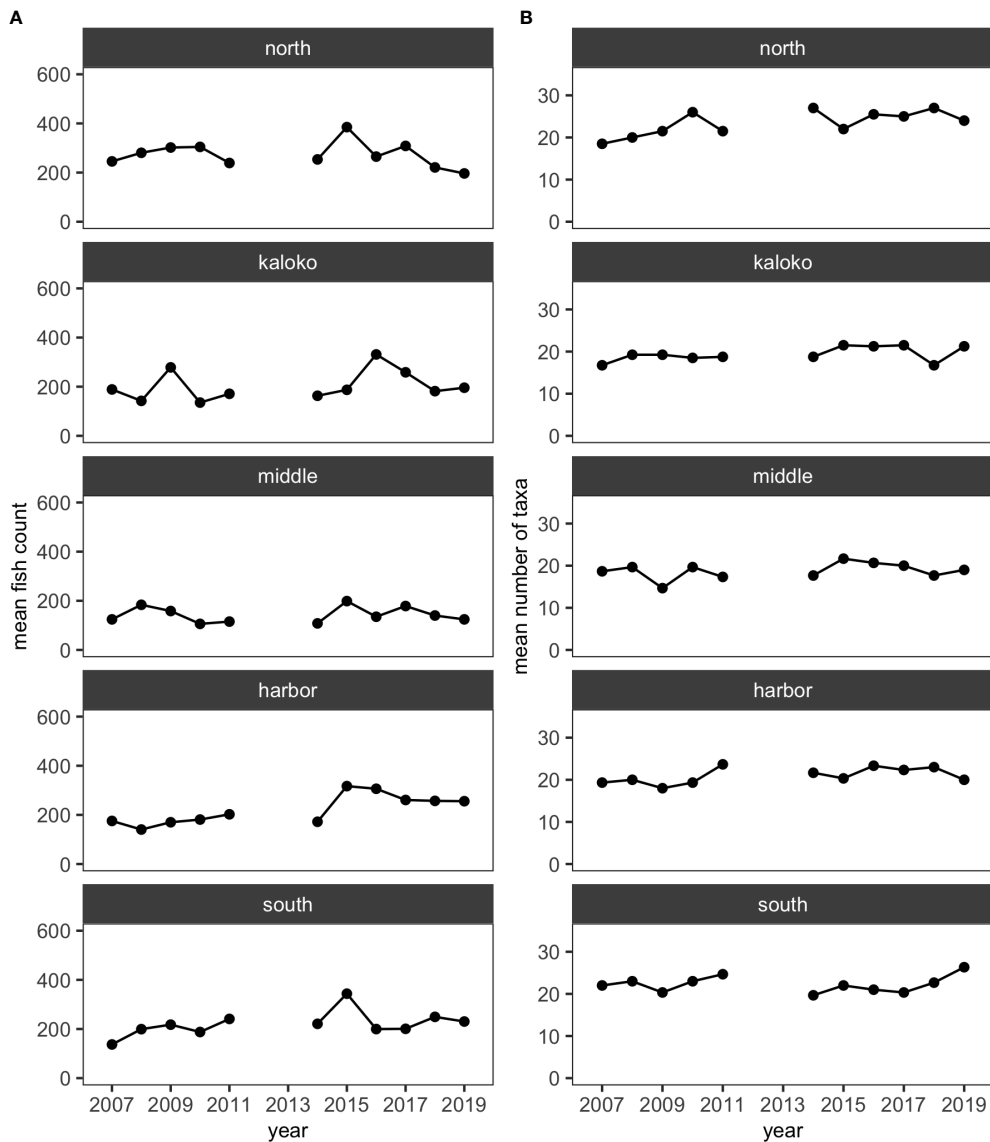


FIGURE 2

Plots showing (A) the mean numbers of fish counts and (B) the mean numbers of fish taxa in each of the five regions in KAHO using the reduced dataset.

confirmed a gradual shift in fish assemblages in each region (Figure S1).

Fish species that were consistently present in high abundance in typical years were relatively similar among different regions, although some differences were detected (Table 2). For example, *Chromis vanderbilti* was highly abundant in the North, Kaloko and Middle regions but not in the Harbor and South regions. *Ctenochaetus strigosus* was also highly abundant in the North, Kaloko, Harbor and South regions but not in the Middle region. The Harbor region was somewhat distinct from all other regions due to higher abundances of the corallivores *Chaetodon multicinctus* and *Plectroglyphidodon*

johnstonianus and lower abundances of *C. vanderbilti*, *Acanthurus nigrofuscus* than the other regions.

The changes in fish assemblages that were identified as outside natural variability by MCCs were mostly due to changes in abundances of common species, such as *Chromis agilis*, *C. vanderbilti*, *A. nigrofuscus*, *C. strigosus* and *Zebriasoma flavescens* (Table 3). Some notable and consistent changes in fish assemblages included decreases in the abundances of the genus *Chromis* and increases in the abundances of the genus *Abudefduf* in the North region, increases in the abundance of *C. agilis* in the Kaloko and Middle regions (i.e., middle section of KAHO) and decreases elsewhere, decreases in the abundances of *C. strigosus*

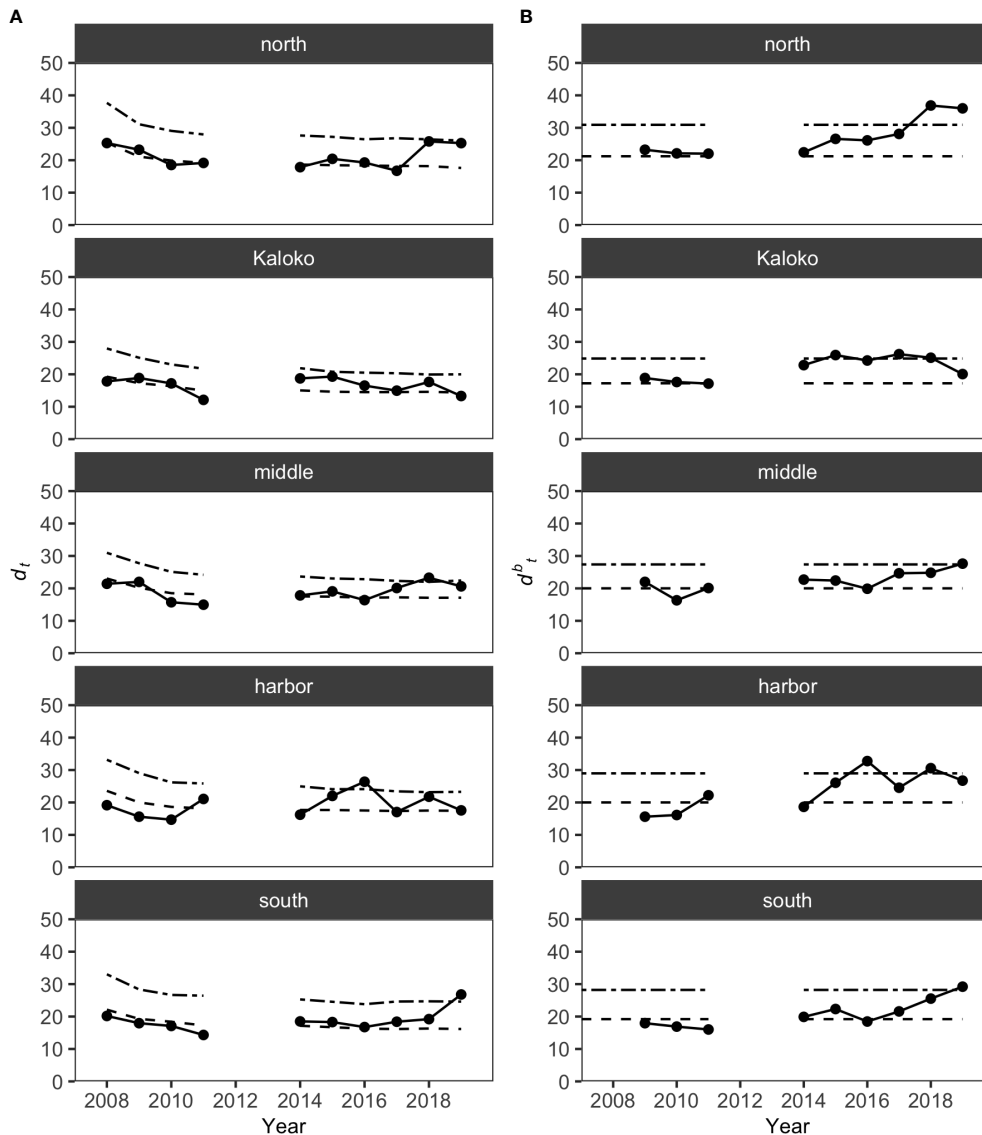


FIGURE 3 Results of MCCs for KALO fish assemblages showing (A) d_t values and (B) d_t^p values. Dashed lines on each plot show 50 percentile confidence bounds as representations of the temporal trends, and dash-dotted lines show 95 percentile confidence bounds as upper confidence limits under which the status of the regions were considered stable or within natural variability.

in the Middle and South regions and increases in the abundance of *Z. flavescens* in the Harbor region.

KALA

Over the 14 years of the study, 39,091 individuals of reef fishes belonging to 138 taxonomic groups (136 species and 2 groups identified to genus), excluding pelagic and semi-pelagic species, were identified along the 15 fixed transects. Similar to KALO, a little over half of these groups did not

account for 3% or more of fish abundance in any surveys. Excluding less-common species generated a smaller dataset with 38,047 individuals belonging to 62 species and one genus group for analysis. The mean number of species and fish counts were relatively stable at each region (i.e., West, West Peninsula, Northwest Peninsula, Peninsula, East Peninsula and East) and did not visually show any obvious trends (Figure 4).

MCCs detected two potentially anomalous years in the structure of KALA fish assemblages on the basis of the Bray-Curtis measure; d_t and d_t^p values exceeded the upper confidence

limit in 2014 in all regions except for the West Peninsula region and in 2015 in the West region (Figure 5). The West Peninsula region also had a d_t^b value exceeding the upper confidence limit in 2009, and this was due to a decrease in the overall fish count as observed in the dips in the total fish count and the number of fish taxa in the region (Figure 4). Fish taxa that were consistently present in high abundance during typical years as identified by MCCs were slightly more variable among regions than those in KAHO. Some common taxa were, however, consistently found at multiple regions, and these included *A. nigrofuscus*, *C. vanderbilti*, *C. strigosus*, *Sufflamen bursa* and *Thalassoma duperrey* (Table 4). *C. vanderbilti* was particularly abundant from the Northwest Peninsula to the East Peninsula and had considerable contributions to the within-group similarities in the regions (Table 4).

Overall, the 2014 anomaly was characterized by increases in the abundance of *Acanthurus* (*A. blochii*, *A. leucopareius*, *A. nigrofuscus*, *A. thompsoni* and *A. triostegus*) and *Ctenochaetus strigosus* (Table 5). On the other hand, the 2015 anomaly in the West region was due to no observations of *C. vanderbilti* (the

most numerically abundant fish species in the West region in non-anomalous years), decreases in the abundances of *T. duperrey* and *Parupeneus multifasciatus* and an increase in the abundance of *C. verater* (Table 6). The corallivore *P. johnstonianus* was also not detected in 2015, resulting in a decrease when being compared with the 2006 and 2007 baseline data (Table 6), but this species was never consistently abundant and was not detected in the region in 2011 and from 2014 to 2019.

Discussion

The coral reefs in the two parks in the present study experience different natural and anthropogenic disturbances. Although they are both in a degraded state in comparison to reefs in the uninhabited Northwestern Hawaiian Islands (Friedlander et al., 2018), KALA is relatively inaccessible due to its remoteness, and receives minimal fishing pressure whereas KAHO is highly accessible for recreational and commercial uses,

TABLE 2 Results of SIMPER analysis showing the top five species that were consistently present in high abundance in each region of KAHO in "typical" years identified by MCCs.

	Top 5 species	Square-root abundance	Similarity	Similarity/SD
North (2007 – 2017)	<i>Chromis vanderbilti</i>	8.89	10.08	1.11
	<i>Ctenochaetus strigosus</i>	3.94	5.65	3.62
	<i>Acanthurus nigrofuscus</i>	3.51	5.20	3.88
	<i>Zebrasoma flavescens</i>	3.52	5.03	4.21
	<i>Chromis agilis</i>	5.96	4.75	0.71
Kaloko (2007 – 2011)	<i>Chromis vanderbilti</i>	7.93	12.84	2.10
	<i>Ctenochaetus strigosus</i>	4.03	8.42	6.62
	<i>Acanthurus nigrofuscus</i>	3.50	6.85	3.88
	<i>Zebrasoma flavescens</i>	2.98	5.32	2.80
	<i>Paracirrhites arcatus</i>	2.04	3.92	3.29
Middle (2007 – 2017)	<i>Chromis vanderbilti</i>	6.71	11.98	2.42
	<i>Acanthurus nigrofuscus</i>	3.46	6.66	2.48
	<i>Thalassoma duperrey</i>	2.15	4.57	3.37
	<i>Zebrasoma flavescens</i>	2.05	4.05	3.02
	<i>Chromis agilis</i>	2.95	3.01	0.87
Harbor (2007 – 2014)	<i>Chromis agilis</i>	7.86	13.98	4.28
	<i>Ctenochaetus strigosus</i>	4.96	10.21	9.21
	<i>Zebrasoma flavescens</i>	5.12	10.21	6.12
	<i>Chaetodon multicinctus</i>	2.58	4.78	3.18
	<i>Plectroglyphidodon johnstonianus</i>	1.76	83.54	5.85
South (2007 – 2017)	<i>Zebrasoma flavescens</i>	4.01	6.65	4.32
	<i>Ctenochaetus strigosus</i>	4.10	6.50	2.87
	<i>Acanthurus nigrofuscus</i>	3.74	5.98	3.43
	<i>Chromis agilis</i>	5.25	5.47	0.83
	<i>Thalassoma duperrey</i>	2.31	4.09	4.23

The years included in the analysis are shown in the parentheses under each region name. The mean square-root abundance of each taxon in each region (square-root abundance), the contribution (i.e., mean similarity) of each taxon to the overall Bray-Curtis similarity for the region (similarity) and the ratio of the mean similarity to standard deviation (similarity/SD) are also shown. Average similarity of each region was 55.90 for North, 65.19 for Kaloko, 56.60 for Middle, 63.58 for Harbor and 55.03 for South.

TABLE 3 Results of SIMPER analysis showing the top five species that contributed to separating fish assemblages of KAHO in anomalous years as identified by MCCs.

	Top 5 species	Square-root abundance	Square-root abundance in years being compared	Dissimilarity
North 2018 vs. previous years	<i>Chromis vanderbilti</i> (-)	7.55	8.89	4.93
	<i>Chromis agilis</i> (-)	2.60	5.96	4.60
	<i>Abudefduf vaigiensis</i> (+)	2.50	1.04	2.18
	<i>Acanthurus thompsoni</i> (-)	1.32	2.65	2.07
	<i>Abudefduf abdominalis</i> (+)	2.24	0.67	1.89
North 2018 vs. baseline	<i>Chromis vanderbilti</i> (-)	7.55	9.65	6.12
	<i>Chromis agilis</i> (-)	2.60	5.28	4.35
	<i>Abudefduf vaigiensis</i> (+)	2.50	0.00	2.26
	<i>Abudefduf abdominalis</i> (+)	2.24	0.00	2.02
	<i>Paracirrhites arcatus</i> (-)	0.00	2.03	1.86
North 2019 vs. baseline	<i>Chromis vanderbilti</i> (-)	7.61	9.65	6.23
	<i>Chromis agilis</i> (-)	3.32	5.28	4.66
	<i>Abudefduf vaigiensis</i> (+)	2.74	0.00	2.60
	<i>Abudefduf abdominalis</i> (+)	2.18	0.00	2.07
	<i>Monotaxis grandoculis</i> (+)	2.00	0.00	1.94
Kaloko 2015 vs. baseline	<i>Chromis agilis</i> (+)	6.33	2.76	5.75
	<i>Chromis vanderbilti</i> (-)	3.55	8.24	5.36
	<i>Zebrasoma flavescens</i> (+)	5.07	2.40	3.32
	<i>Acanthurus nigrofuscus</i> (+)	4.40	3.07	1.79
	<i>Scarus psittacus</i> (-)	0.35	1.55	1.71
Kaloko 2017 vs. baseline	<i>Chromis agilis</i> (+)	8.54	2.76	7.16
	<i>Chromis vanderbilti</i> (-)	4.55	8.24	6.10
	<i>Ctenochaetus strigosus</i> (+)	5.89	3.71	2.46
	<i>Zebrasoma flavescens</i> (+)	4.05	2.40	2.38
	<i>Acanthurus nigrofuscus</i> (+)	4.90	3.07	2.13
Kaloko 2018 vs. baseline	<i>Chromis agilis</i> (+)	7.95	2.76	7.30
	<i>Chromis vanderbilti</i> (-)	5.09	8.24	5.35
	<i>Zebrasoma flavescens</i> (+)	3.68	2.40	1.98
	<i>Scarus psittacus</i> (-)	0.00	1.55	1.78
	<i>Plectroglyphidodon johnstonianus</i> (-)	0.35	1.47	1.55
Middle 2018 vs. previous years	<i>Chromis agilis</i> (+)	4.77	2.95	5.22
	<i>Chromis vanderbilti</i> (-)	5.98	6.71	3.71
	<i>Ctenochaetus strigosus</i> (-)	1.25	2.23	2.73
	<i>Melichthys niger</i> (+)	1.63	0.70	2.62
	<i>Acanthurus nigrofuscus</i> (-)	2.46	3.46	1.94
Middle 2019 vs. baseline	<i>Chromis vanderbilti</i> (-)	7.23	7.47	4.67
	<i>Chromis agilis</i> (+)	2.68	2.37	3.01
	<i>Ctenochaetus strigosus</i> (-)	1.60	2.14	2.88
	<i>Paracirrhites arcatus</i> (-)	0.00	1.81	2.58
	<i>Acanthurus olivaceus</i> (-)	0.00	1.97	2.46
Harbor 2016 vs. previous years	<i>Zebrasoma flavescens</i> (+)	9.72	5.31	4.08
	<i>Ctenochaetus strigosus</i> (+)	7.26	4.84	2.26
	<i>Chromis agilis</i> (-)	7.18	7.72	2.03
	<i>Abudefduf abdominalis</i> (+)	2.38	0.07	2.03
	<i>Melichthys niger</i> (+)	2.25	0.65	1.96
Harbor 2016 vs. baseline	<i>Zebrasoma flavescens</i> (+)	9.72	4.57	4.88
	<i>Chromis agilis</i> (-)	7.18	7.76	2.66

(Continued)

TABLE 3 Continued

	Top 5 species	Square-root abundance	Square-root abundance in years being compared	Dissimilarity
Harbor 2018 vs. baseline	<i>Ctenochaetus strigosus</i> (+)	7.26	4.56	2.57
	<i>Melichthys niger</i> (+)	2.25	0.00	2.14
	<i>Abudefduf abdominalis</i> (+)	2.38	0.00	2.07
	<i>Chlorurus spilurus</i> (+)	4.32	0.64	3.68
	<i>Zebrasoma flavescens</i> (+)	8.03	4.57	3.52
	<i>Chromis agilis</i> (-)	7.22	7.76	2.90
	<i>Melichthys niger</i> (+)	2.61	0.00	2.66
	<i>Chaetodon lunula</i> (+)	2.31	0.33	2.29
South 2019 vs. previous years	<i>Chromis vanderbilti</i> (+)	10.41	4.51	6.36
	<i>Chromis agilis</i> (-)	2.86	5.33	4.25
	<i>Ctenochaetus strigosus</i> (-)	2.14	4.14	2.31
	<i>Abudefduf abdominalis</i> (-)	1.56	1.90	2.30
	<i>Zebrasoma flavescens</i> (-)	3.07	4.20	1.95
South 2019 vs. baseline	<i>Chromis vanderbilti</i> (+)	10.41	3.99	6.87
	<i>Chromis agilis</i> (-)	2.86	4.74	3.83
	<i>Ctenochaetus strigosus</i> (-)	2.14	3.50	2.11
	<i>Chromis verater</i> (-)	0.00	1.92	1.81
	<i>Abudefduf abdominalis</i> (+)	1.56	1.16	1.78

The anomalous years were compared with all previous years or the baseline years (i.e., 2007 and 2008) depending on the results of MCCs. The mean square-root abundance of each taxon in each region (square-root abundance), the mean square-root abundance of each taxon in either all the previous years or the baselines years (square-root abundance in years being compared) and the contribution (i.e., mean dissimilarity) of each taxon to the overall Bray-Curtis dissimilarity are also shown. Increases (+) or decreases (-) of the taxa are shown in parentheses.

is influenced by adjacent land use, groundwater and runoff (Brown et al., 2016; Gove et al., 2019) and impacted by the global-scale bleaching event in 2015. Here we employed MCCs and detected two types of anomalies in the fish assemblages at KAHO and KALA: 1) gradual shifts in the KAHO fish assemblages in recent years that were better captured by d_t^b values, and 2) changes in the KALA fish assemblages in 2014 and, to a lesser extent, 2015 that were captured by both d_t and d_t^b values. MCCs are a relatively new approach to analyzing fish assemblages (Anderson and Thompson, 2004), and a modified version of this approach has been previously applied to fish assemblages in Hawai'i (Fukunaga and Kosaki, 2017). This technique statistically tests for temporal changes within a site that are beyond natural variability. In both cases, the anomalies in the present study were characterized by changes (i.e., both increases and decreases) in relative abundances of numerically dominant fish species such as *Chromis agilis*, *Chromis vanderbilti*, *Acanthurus nigrofuscus*, *Ctenochaetus strigosus* and *Zebrasoma flavescens*.

In KALA, changes in species abundance that contributed to the 2014 anomaly were consistent across regions. The abundances of *Acanthurus* (*A. blochii*, *A. leucopareius*, *A. nigrofuscus*, *A. thompsoni* and *A. triostegus*) and *C. strigosus* all increased. There are some accounts that 2014 was an exceptionally good recruitment year for some fishes in the

main Hawaiian Islands (e.g., *C. strigosus* and *Z. flavescens* in west Hawai'i Island; Walsh et al., 2019). *Post-hoc* analyses comparing the size frequency of these fishes between years prior to 2014 and year 2014 clearly show large increases in the proportion of juvenile abundance in 2014 for both *Acanthurus* spp. (Figure S2A) and *C. strigosus* (Figure S2B). As no such anomaly was detected in KAHO in 2014, the recruitment event was potentially site specific. To our knowledge, this was the first study to document the recruitment event on another Hawaiian Island besides Hawai'i (Walsh et al., 2019). The species identification of the recruits in the present study can facilitate the understanding of the spatial extent of the event through analysis of existing reef monitoring data throughout Hawai'i. For the 2015 anomaly in the West region, the complete disappearance of *C. vanderbilti* is somewhat inexplicable, but their abundance returned to the typical level in subsequent years. A shift in the distribution of *C. vanderbilti* has been previously reported in response to a storm disturbance (Walsh, 1983), so their temporary disappearance in the West region might be a response to an unknown localized physical condition. *C. vanderbilti* also often occurs in aggregation (Randall, 2007), so it is possible that there happened to be no *C. vanderbilti* along the two transects in the region in that particular year. The absence of *C. vanderbilti* in the entire West region during the 2015 season, however, is further supported by the lack of this

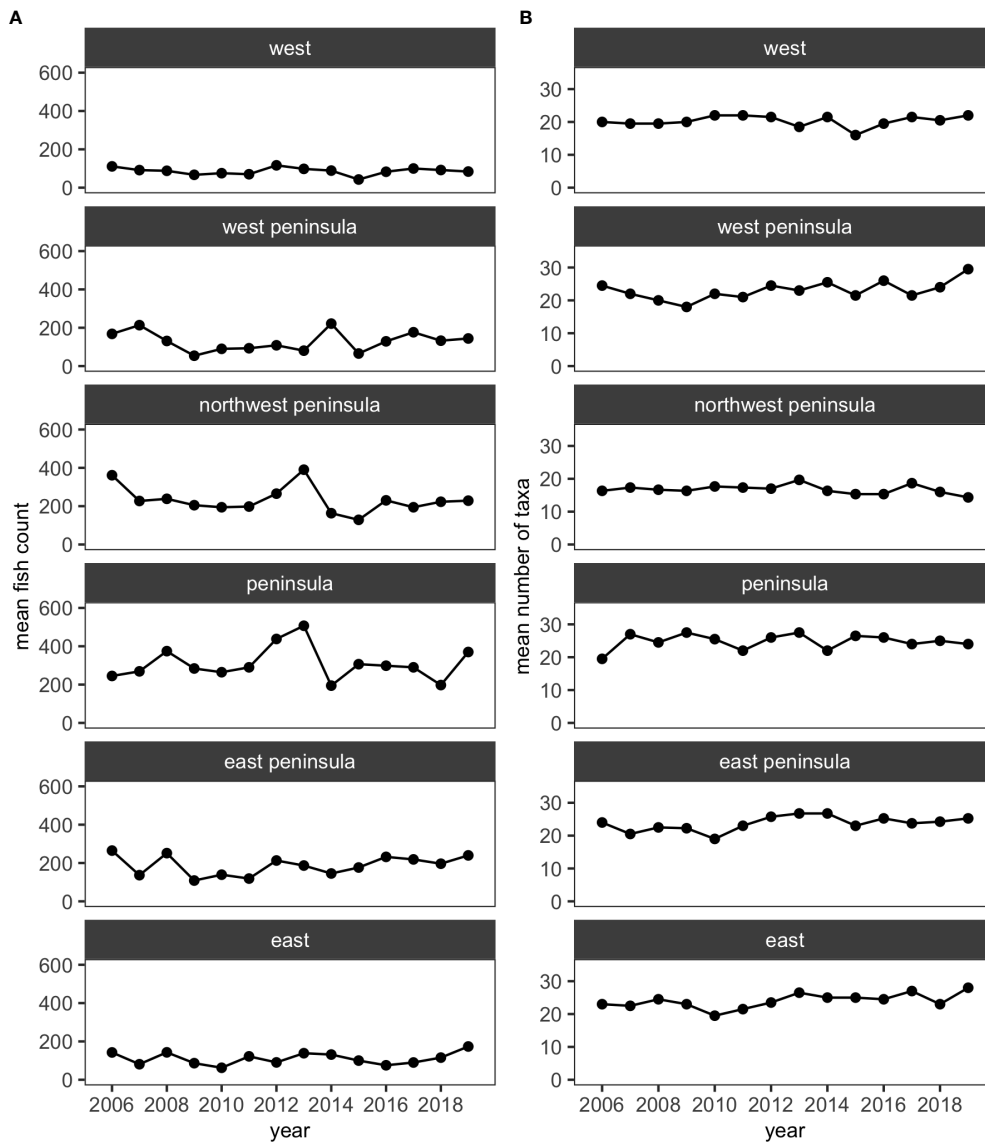


FIGURE 4 Plots showing (A) the mean numbers of fish counts and (B) the mean numbers of fish taxa in each of the five regions in KALA using the reduced dataset.

species on the three temporary transects that were in close proximity (0.5 – 1.0 km) to the fixed transects in that year (Brown et al., 2022).

In KAHO, there were no obvious patterns detected across the regions or habitat types that explained the changes in species abundance in anomalous years, but the changes were mostly consistent within each region across years. This observation confirms that the gradual shifts captured by d^b_t values in KAHO were likely trends occurring within individual regions rather than turnover of various species that happened to occur over consecutive years. Mechanisms of the shifts are unclear but may be partly related to the 2015 mass coral bleaching (e.g., Olsen

et al., 2022). For example, the 2015 bleaching event resulted in complete loss of the branching coral *Pocillopora meandrina* along the 15 fixed transects (McCutcheon and McKenna, 2021), and *P. meandrina* was relatively abundant in the North (Site 01; Table 1) and South (Site 15; Table 1) regions. Therefore, the observed shifts in the fish assemblages in these two regions could be a delayed effect of the bleaching event as the branching structure of *P. meandrina* slowly eroded over time. In the North region, decreases in the abundance of *Paracirrhites arcatus*, which utilizes pocilloporids as their preferred habitat (Coker et al., 2015), contributed to the shift in the structure of fish assemblage in 2018 (Table 3). Further *post-hoc* investigations

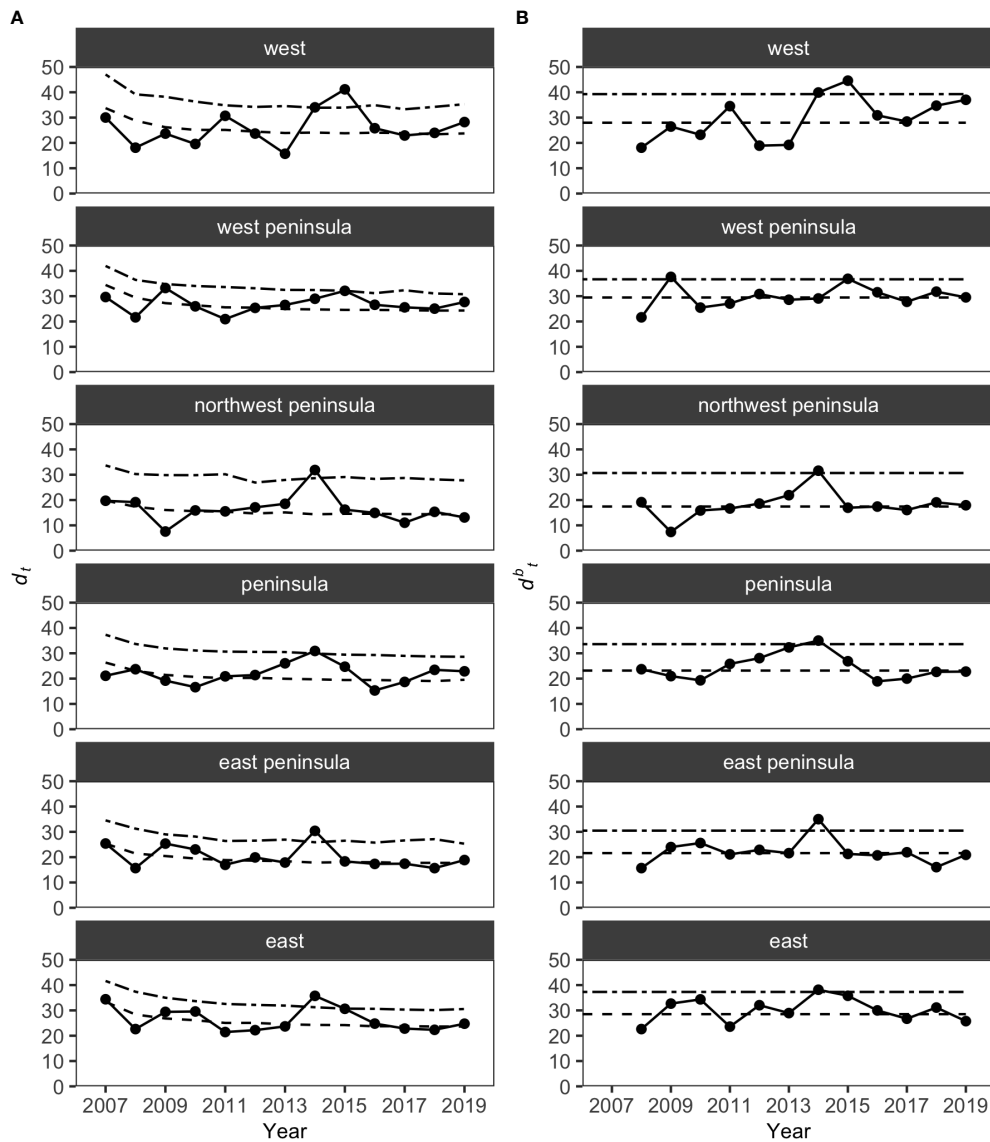


FIGURE 5 Results of MCCs for KALA fish assemblages showing (A) d_t values and (B) d^p_t values. Dashed lines on each plot show 50 percentile confidence bounds as representations of the temporal trends, and dash-dotted lines show 95 percentile confidence bounds as upper confidence limits under which the status of the regions were considered stable or within natural variability.

reveal that the abundance of *P. arcatus* at Site 01 was, on average, 6.5 individuals per transect before the bleaching event but reduced to 2-3 individuals after the bleaching then to no individuals in 2018 and 2019. Similarly, *P. arcatus* abundance at Site 15 decreased from 6.8 individuals on average before the bleaching event to 0-2 individuals after the bleaching event, even though this species was not among the top five species contributing to the observed shift in the South region.

Although decreases in fish abundance and diversity are often reported following coral bleaching events (Pratchett et al., 2011), there was no clear decrease in either the total fish counts or the

number of fish taxa corresponding to the shifts in fish assemblages in KAHO (Figure 2). Corallivores are generally susceptible to coral loss and degradation of reef habitats due to their coral dependency (Pratchett et al., 2011; Magel et al., 2020). Unlike other trophic groups whose distributions are associated with habitat structure, abundances of corallivores are affected by both habitat structure and live coral cover (Fukunaga et al., 2020); thus more immediate responses could be expected from corallivores than other trophic groups that respond to structural changes of coral reefs. In the Harbor region of KAHO where the two corallivores *Chaetodon multicinctus* and *Plectrogliphidodon*

TABLE 4 Results of SIMPER analysis showing the top five species that were consistently present in high abundance in each region of KALA in “typical” years identified by MCCs.

	Top 5 species	Square-root abundance	Similarity	Similarity/SD
West (2006 – 2013 & 2016 – 2019)	<i>Chromis vanderbilti</i>	4.62	7.94	1.47
	<i>Paracirrhites arcatus</i>	2.47	6.18	5.95
	<i>Thalassoma duperrey</i>	2.12	4.96	2.61
	<i>Acanthurus nigrofuscus</i>	1.96	4.40	2.82
	<i>Sufflamen bursa</i>	1.73	4.07	4.83
West Peninsula (2006 – 2008 & 2010 – 2014 & 2016 – 2019)	<i>Acanthurus nigrofuscus</i>	3.17	5.84	5.50
	<i>Paracirrhites arcatus</i>	2.94	5.70	2.98
	<i>Chromis ovalis</i>	4.10	5.50	1.15
	<i>Thalassoma duperrey</i>	2.48	5.09	4.24
	<i>Kyphosus</i> sp.	4.15	3.83	0.97
Northwest Peninsula (2006 – 2013 & 2015 – 2019)	<i>Chromis vanderbilti</i>	11.72	20.90	3.69
	<i>Paracirrhites arcatus</i>	3.50	8.07	3.16
	<i>Thalassoma duperrey</i>	3.68	7.95	3.00
	<i>Acanthurus nigrofuscus</i>	1.73	2.18	0.92
	<i>Sufflamen bursa</i>	1.09	1.91	0.84
Peninsula (2006 – 2013 & 2015 – 2019)	<i>Chromis vanderbilti</i>	12.93	18.09	4.08
	<i>Kyphosus</i> sp.	4.23	6.16	2.91
	<i>Thalassoma duperrey</i>	2.58	4.07	4.88
	<i>Ctenochaetus strigosus</i>	2.57	4.00	3.85
	<i>Acanthurus leucopareius</i>	2.98	3.71	3.41
East Peninsula (2006 – 2013 & 2015 – 2019)	<i>Chromis vanderbilti</i>	8.34	12.06	2.00
	<i>Acanthurus nigrofuscus</i>	3.35	6.13	5.43
	<i>Paracirrhites arcatus</i>	2.69	5.00	4.04
	<i>Ctenochaetus strigosus</i>	2.77	4.85	4.02
	<i>Thalassoma duperrey</i>	2.53	4.06	2.99
East (2006 – 2013 & 2016 – 2019)	<i>Thalassoma duperrey</i>	2.42	4.98	3.16
	<i>Parupeneus multifasciatus</i>	2.10	4.28	4.78
	<i>Sufflamen bursa</i>	2.14	4.04	2.96
	<i>Halichoeres ornatissimus</i>	1.97	3.93	2.93
	<i>Acanthurus nigrofuscus</i>	2.04	3.53	1.83

The years included in the analysis are shown in the parentheses under each region name. The mean square-root abundance of each taxon in each region (square-root abundance), the contribution (i.e., mean similarity) of each taxon to the overall Bray-Curtis similarity for the region (similarity) and the ratio of the mean similarity to standard deviation (similarity/SD) are also shown. Average similarity of each region was 53.10 for West, 54.44 for West Peninsula, 55.40 for Northwest Peninsula, 61.13 for Peninsula, 54.42 for East Peninsula and 53.12 for East.

johnstonianus were consistently present in high abundance in non-anomalous years, no large decreases in their abundances were observed after the bleaching in 2015 (Table 3). There was a decrease in the abundance of *P. johnstonianus* in Kaloko, the other region with high coral cover, but this occurred only in 2018 (Table 3). The lack of clear effects of bleaching on corallivores in the Kaloko and Harbor regions are likely due to the high abundance of *Porites* corals (Table 1), which were not affected by the 2015 bleaching event as severely as *P. meandrina* (McCutcheon and McKenna, 2021).

Despite the existing press disturbances from aquatic commercial and recreational activities and adjacent land use in KAHO, and documented negative impacts of such disturbances on fish assemblages in Hawai'i (DeMartini et al., 2013; Foo et al.,

2021) and elsewhere (Chabanet et al., 1995; Arias-Godínez et al., 2019), there were no clear declining trends in the fish assemblages associated with the anomalies. The direction of changes in species abundance was not consistent across regions in KAHO (e.g., *C. vanderbilti* decreasing in the North and Kaloko regions but increasing in the South region and *C. strigosus* increasing in the Kaloko and Harbor regions but decreasing in the Middle and South regions). This suggests that the shift in the fish assemblage in each region could be the result of local anthropogenic factors specific to the region, as well as potential interactions of multiple local factors having varying effects on different fish species. Such mixed responses of reef fishes to disturbance events have previously been shown through meta-analysis by Wilson et al. (2006). In that study, the negative

TABLE 5 Results of SIMPER analysis showing the top five species that contributed to separating fish assemblages of KALA in 2014 years as identified by MCCs.

	Top 5 species	Square-root abundance	Square-root abundance in years being compared	Dissimilarity
West 2014 vs. baseline	<i>Chromis vanderbilti</i> (-)	3.29	5.63	5.36
	<i>Acanthurus thompsoni</i> (+)	2.40	0.00	3.35
	<i>Acanthurus nigrofuscus</i> (+)	3.74	1.52	3.15
	<i>Ctenochaetus strigosus</i> (+)	2.00	0.00	2.80
	<i>Naso hexacanthus</i> (+)	1.82	0.25	2.24
Northwest Peninsula 2014 vs. previous years	<i>Chromis vanderbilti</i> (-)	5.44	12.22	7.89
	<i>Acanthurus nigrofuscus</i> (+)	5.71	1.79	5.10
	<i>Kyphosus</i> sp. (+)	3.73	1.08	4.74
	<i>Ctenochaetus strigosus</i> (+)	2.48	0.72	2.49
	<i>Cirrhitops fasciatus</i> (+)	2.08	0.84	1.85
Northwest Peninsula 2014 vs. baseline	<i>Chromis vanderbilti</i> (-)	5.44	12.75	8.02
	<i>Acanthurus nigrofuscus</i> (+)	5.71	1.84	5.25
	<i>Kyphosus</i> sp. (+)	3.73	1.70	5.05
	<i>Ctenochaetus strigosus</i> (+)	2.48	0.71	2.49
	<i>Cirrhitops fasciatus</i> (+)	2.08	0.83	1.89
Peninsula 2014 vs. previous years	<i>Chromis vanderbilti</i> (-)	8.62	14.34	5.36
	<i>Acanthurus nigrofuscus</i> (+)	6.32	1.78	4.34
	<i>Acanthurus blochii</i> (+)	3.08	0.53	2.88
	<i>Kyphosus</i> sp. (-)	2.00	4.04	1.99
	<i>Lutjanus kasmira</i> (-)	0.00	2.21	1.97
Peninsula 2014 vs. baseline	<i>Acanthurus nigrofuscus</i> (+)	6.32	1.35	5.09
	<i>Chromis vanderbilti</i> (-)	8.62	12.19	4.19
	<i>Kyphosus</i> sp. (-)	2.00	5.62	3.73
	<i>Acanthurus blochii</i> (+)	3.08	0.50	3.06
	<i>Lutjanus kasmira</i> (-)	0.00	2.03	1.91
East Peninsula 2014 vs. previous years	<i>Chromis vanderbilti</i> (-)	2.88	8.12	5.77
	<i>Acanthurus nigrofuscus</i> (+)	6.87	3.06	4.10
	<i>Acanthurus triostegus</i> (+)	2.00	0.81	2.43
	<i>Acanthurus leucopareius</i> (+)	2.22	1.27	1.99
	<i>Ctenochaetus strigosus</i> (+)	4.40	2.59	1.95
East Peninsula 2014 vs. baseline	<i>Chromis vanderbilti</i> (-)	2.88	9.23	6.63
	<i>Acanthurus nigrofuscus</i> (+)	6.87	2.99	4.13
	<i>Acanthurus triostegus</i> (+)	2.00	1.54	2.78
	<i>Acanthurus leucopareius</i> (+)	2.22	1.22	2.31
	<i>Ctenochaetus strigosus</i> (+)	4.40	2.70	1.87
East 2014 vs. previous years	<i>Acanthurus leucopareius</i> (+)	4.24	1.54	4.60
	<i>Acanthurus nigrofuscus</i> (+)	4.94	1.58	3.84
	<i>Chromis vanderbilti</i> (-)	1.41	3.05	3.68
	<i>Chromis ovalis</i> (+)	2.12	1.76	2.75
	<i>Stethojulis balteata</i> (-)	0.00	1.67	1.88
East 2014 vs. baseline	<i>Chromis vanderbilti</i> (-)	1.41	4.33	5.03
	<i>Acanthurus leucopareius</i> (+)	4.24	1.49	4.63
	<i>Acanthurus nigrofuscus</i> (+)	4.94	2.03	3.34
	<i>Chromis ovalis</i> (+)	2.12	1.30	2.36
	<i>Scarus rubroviolaceus</i> (+)	1.62	0.90	1.94

The assemblages in 2014 were compared with those in all previous years or the baseline years (i.e., 2006 and 2007) depending on the results of MCCs. The mean square-root abundance of each taxon in each region (square-root abundance), the mean square-root abundance of each taxon in either all the previous years or the baselines years (square-root abundance in years being compared) and the contribution (i.e., mean dissimilarity) of each taxon to the overall Bray-Curtis dissimilarity are also shown. Increases (+) or decreases (-) of the taxa are shown in parentheses.

impacts of coral losses were relatively consistent among corallivores and coral-dwelling fishes, but effects on other trophic groups varied depending on types of disturbances (loss of live coral tissue vs. habitat complexity), individual study locations, and fish species.

The long-term fish monitoring data from the two national parks in the present study showed the relatively stable state of the KALA fish assemblages and recent shifts in KAHO fish assemblages and offer important baseline information for future monitoring and management activities for each park. Using MCCs with a new dataset each year will allow managers to quickly identify temporal shifts in the fish assemblages that are beyond natural variability and to trigger more detailed investigations into potential causes, including the identities of fish species responsible for the shifts and potential environmental factors contributing to the shifts. Despite the relatively small spatial extent of 2.4 km², KAHO experiences a variety of local anthropogenic pressures, and the levels may vary among the regions within the park. While isolating the effects of individual local factors or separating the effects of coral bleaching and local anthropogenic factors could be difficult due to their potential interactions, mapping the spatial extent of potential impacts of each local factor inside the marine area can help identify the primary concerns for each region, facilitating region-specific analyses between the fish assemblage and environmental variables. An additional component to reconstruct the reefs in three dimensions using photogrammetric techniques has recently been added to the monitoring program, and this allows for quantification of structural loss separate from live coral loss. As localized

thermal stress events were detected in both KAHO and KALA in 2019 (McCutcheon and McKenna, 2021), continuous monitoring of these two parks is critical to assess how the coral reefs ecosystems under two different regimes respond to repeated thermal and other disturbance stress events.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: <https://irma.nps.gov/Portal>.

Ethics statement

The monitoring surveys were conducted under the permits, KAHO-2014-SCI-0006, KAHO-2016-SCI-0009, KAHO-2019-SCI-0002 and KALA-2013-SCI-0007, issued by the National Park Service.

Author contributions

AF and JB conceived the ideas behind the manuscript, and all authors made substantial intellectual contributions to develop the manuscript. SM, EB and AM collected the data. AF analysed

TABLE 6 Results of SIMPER analysis showing the top five species that contributed to separating fish assemblages of KALA in 2015 years as identified by MCCs.

	Top 5 species	Square-root abundance	Square-root abundance in years being compared	Dissimilarity
West 2015 vs. previous years	<i>Chromis vanderbilti</i> (-)	0.00	4.85	7.99
	<i>Chromis verater</i> (+)	2.12	0.41	3.55
	<i>Thalassoma duperrey</i> (-)	0.50	2.01	2.64
	<i>Acanthurus nigrofuscus</i> (+)	2.90	1.93	2.21
	<i>Parupeneus multifasciatus</i> (-)	0.71	1.66	2.00
West 2015 vs. baseline	<i>Chromis vanderbilti</i> (-)	0.00	5.63	5.36
	<i>Chromis verater</i> (+)	2.12	0.43	3.35
	<i>Thalassoma duperrey</i> (-)	0.50	2.26	3.15
	<i>Plectroglyphidodon johnstonianus</i> (-)	0.00	1.49	2.80
	<i>Parupeneus multifasciatus</i> (-)	0.71	1.69	2.24

The assemblages in 2014 were compared with those in all previous years or the baseline years (i.e., 2006 and 2007) depending on the results of MCCs. The mean square-root abundance of each taxon in each region (square-root abundance), the mean square-root abundance of each taxon in either all the previous years or the baselines years (square-root abundance in years being compared) and the contribution (i.e., mean dissimilarity) of each taxon to the overall Bray-Curtis dissimilarity are also shown. Increases (+) or decreases (-) of the taxa are shown in parentheses.

the data and led the writing of the manuscript. All authors contributed to the article and approved the submitted version.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.1038365/full#supplementary-material>

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