REPORT

Coral community resilience to successive years of bleaching in Kāneʻohe Bay, Hawaiʻi

Raphael Ritson-Williams[1,2] · Ruth D. Gates[1]

Abstract The Hawaiian Islands are at the northern edge of coral reef distributions, and corals found there are exposed to large seasonal temperature changes. Historically, coral bleaching in the Hawaiian Islands was extremely rare and had only occurred in 1996. However, in the summers of both 2014 and 2015, successive bleaching events occurred in Kāneʻohe Bay, Oʻahu. Seawater temperatures were above 28 °C for approximately 1 month in 2014 and 3 months in 2015 and peaked above 30 °C in both years. Patterns of bleaching did not vary among the three sites within Kāneʻohe Bay. Severe bleaching and paling covered 77 and 55% of reefs in 2014 and 2015, respectively. Different species showed a range of susceptibility with 80–100% of *Pocillopora spp.* bleaching in both years, but less than 50% bleaching of *Porites compressa* and *Montipora capitata* in Kāneʻohe Bay. Less than 1% of the encrusting coral *Leptastrea purpurea* colonies bleached in both years. Sixty individual colonies of *P. compressa* and *M. capitata* and 28 colonies of *Pocillopora damicornis* were tagged and monitored for rates of bleaching, recovery and mortality throughout the two-year period. Most of the colonies that bleached recovered their symbionts within 3–4 months, though *P. compressa* visually recovered more rapidly than *M. capitata* and *P. damicornis*. Cumulatively, 19% of *P. damicornis*, 10% of *M. capitata* and no *P. compressa* died by May 2016. Partial mortality within a colony did not occur in 2014, but impacted 13% of the colonies in 2015, with *P. damicornis* and *M. capitata* having higher rates of partial mortality than *P. compressa*. Relatively, low susceptibility in the dominant species and low rates of mortality combined with rapid rates of recovery show coral resilience to anomalously high temperatures in Kāneʻohe Bay, Oʻahu.

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Introduction

Climate change is impacting most ecosystems at rapid rates and causing sublethal stress and mortality for many different organisms (Parmesan 2006). Some of the most susceptible animals to climate change are corals, the ecosystem engineers of reefs (Pandolfi et al. 2003; Hoegh-Guldberg et al. 2007). Corals often live close to their upper temperature limits, and as seawater temperatures increase, some corals bleach (Jokiel and Coles 1973; Glynn 1983, 1984). Coral bleaching is a visual paling of coral color associated with the loss of single-celled dinoflagellates from a coral's tissue (Brown 1997; Douglas 2003). This symbiosis is critical to the success and survival of corals (Muscatine and Porter 1977; Goreau et al. 1979), and the breakdown of symbiosis is a sign of sublethal stress that, if not reversed in weeks to months, can result in coral mortality (Glynn 1996; Baker et al. 2008). The condition of individual corals (Brown et al. 2002; Thompson and van

Woesik 2009; Carilli et al. 2012; Howells et al. 2013) and multiple local abiotic conditions (Fitt et al. 2001) all contribute to the susceptibility of corals to bleaching events. However, reefs above 20 degrees latitude are exposed to larger temperature variability than reefs closer to the equator; for instance, the coral reefs of Hawai'i are exposed to a range of annual seawater temperatures from 18 to 29 °C.

Coral bleaching is increasing in frequency as seawater temperatures continue to warm due to climate change (Baker 2003; Hughes et al. 2003; Baker et al. 2008). As technology has advanced, we are better able to predict bleaching events and predict bleaching across wide geographic scales using satellite data (Donner et al. 2005; Liu et al. 2014; Logan et al. 2014). These tools are a useful method to quantify the extent of regional bleaching, but we still know very little about the variation in bleaching within and among coral populations. The overwhelming trend on reefs after a bleaching event is an extensive reduction in the live percent cover of corals (Edwards et al. 2001; Loya et al. 2001), and recovery can take 5–10 yr after a bleaching event (Golbuu et al. 2007; Diaz-Pulido et al. 2009; Gilmour et al. 2013). Some corals bleach but recover their symbionts within months without dying (Levitan et al. 2014; Guest et al. 2016). As seawater temperatures increase around the world, we must understand the features of a "refuge" habitat that enable corals to resist and or rapidly recover from bleaching if we hope to maintain reef ecosystems.

For modern corals, in situ refugia can be defined as a site that coral populations can retreat to, survive in and expand from during environmental change (Ashcroft 2010; Cacciapaglia and van Woesik 2015). Even though there have been extensive laboratory studies to understand the cellular and organismal impacts of bleaching (reviewed in Baker 2003), there has been relatively little documentation on individual populations that resist and recover from changing conditions in modern refugia (Coles and Brown 2003; Edmunds and Gates 2008; Palumbi et al. 2014; Cacciapaglia and van Woesik 2015). Some coral populations are hypothesized to increase resistance to bleaching through consecutive events separated by 3–10 yr (Maynard et al. 2008; Guest et al. 2012; Pratchett et al. 2013). Understanding the population dynamics of corals in refugia will provide researchers with important data on the future trajectory of coral populations and whether they can persist in the face of climate change.

Both resistance to stressful events and the patterns and rates of recovery from stress are critical to understanding resilience (Hodgson et al. 2015). But resistance and recovery are difficult to quantify with typical reef surveys that only provide a snapshot in time. Assessing rates of bleaching susceptibility among individuals, among species and among reef areas are necessary to accurately document the fate of bleached reefs. Individual coral colonies can be monitored for the rates of bleaching and recovery, but are rarely monitored in a natural setting (Baird and Marshall 2002; Jones et al. 2008). There are extensive laboratory experiments that show that individual corals can resist bleaching by hosting different Symbiodiniaceae (Cunning et al. 2015), having different microbiomes (Littman et al. 2011; Bourne et al. 2016; Rosado et al. 2019), different feeding strategies (Grottoli et al. 2006) and differential gene expression (Barshis et al. 2013; Kenkel et al. 2013). However, most of these studies use experimental manipulations and we still need better information of individual phenotypes in situ to better predict whether populations will be able to adapt to local and global stressors. As the frequency and extent of bleaching intensifies, coral reef researchers and managers need to understand patterns of individual and population-scale performance to better tease apart corals' resistance to stress and their ability to recovery from stress, both critical components of resilience.

To document the patterns of coral resilience in situ, we studied three patch reefs in Kāne'ohe Bay on the island of O'ahu. Coral reefs in Hawai'i provide an important case study as extreme environments because they experience a large range in seawater temperatures due to their latitude, and the reefs in Kāne'ohe Bay experience large swings in dissolved CO_2 concentrations (Massaro et al. 2012). Before 2014, the only bleaching event recorded in the main Hawaiian Islands was in 1996 (Jokiel and Brown 2004). However, there was an exceptional warming period corresponding with the El Nino in 2014–2016, which caused the highest seawater temperatures on record in 2016 (Blunden et al. 2018) and also caused extensive coral bleaching throughout the world (Eakin et al. 2019). The reefs in Hawai'i experienced elevated seawater temperatures and subsequent coral bleaching in both summers of 2014 and 2015. This study assesses coral resilience at multiple scales, from individual colonies within and among species to community wide extent of bleaching. We describe in situ patterns of bleaching resistance and recovery in both 2014 and 2015, with data for these select coral colonies before, during and after the 2015 thermal stress. We define coral resilience as resisting and recovering from stress, and we document resilience in Kāne'ohe Bay with some individuals that resisted thermal stress and 93% of the coral colonies recovered from consecutive bleaching events in situ. By studying populations in the wild that survive bleaching, this study begins to quantify the key traits of resilient reefs to better manage reef communities for long-term resistance to climate change.

Materials and methods

Sites studied and physical environmental parameters

In September 2014, coral bleaching was observed throughout Kāneʻohe Bay on the east coast of Oʻahu. Field surveys were conducted at three reefs in the bay to characterize the extent of coral bleaching and to document patterns of recovery. Reef 44 is located at the northern end of Kāneʻohe Bay (N 21.476, W 157.834), reef 25 is in the middle bay (N 21.461, W 157.823) and the reef at the northwestern side of the Hawaiʻi Institute of Marine Biology (HIMB) (N 21.436, W 157.792) is located in the southern portion of the bay (Fig. 1). These reefs were selected to encompass a gradient of exposure to different abiotic conditions with reefs in the north of the bay (44) characterized by greater amounts of freshwater input as

well as greater oceanic influence and reefs in the south (HIMB) with less mixing and a longer retention time of seawater (Lowe et al. 2009).

At each of these reefs, abiotic parameters were monitored at 2 m depth. Temperature was recorded every 15 min using a HOBO pendant logger placed inside the cement block so that it was shaded from direct light. The temperature loggers were calibrated together, and a linear regression conversion factor was applied to ensure the data from different loggers were comparable. Photosynthetic active radiation (PAR) was recorded every 15 min using an Odyssey PAR logger. PAR loggers were calibrated in laboratory flow-through seawater tanks by comparison to a Li-Cor model LI-1400 to create a standard curve of μmol s^{-1} m^{-2} using a linear regression equation. Sediment was measured in 5 cm diameter PVC tubes that were capped at the bottom. The tubes were 42 cm long giving a 7:1 ratio of trap height to mouth width. Each sediment tube

Fig. 1 A map of Kāneʻohe Bay showing the locations of the patch reefs studied. The inset shows the location of Kāneʻohe Bay on Oʻahu Hawaiʻi, USA
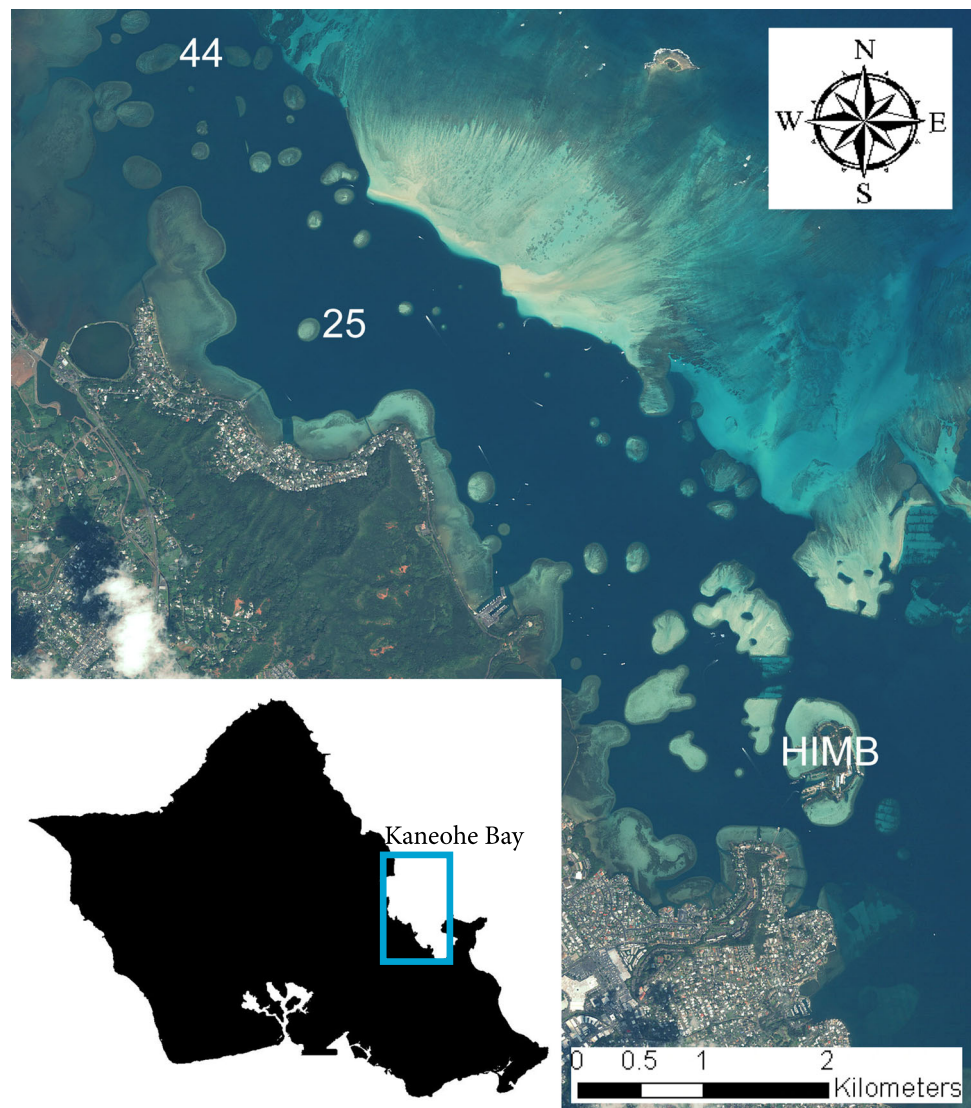
was held upright by the cement block. Each tube was collected monthly, and the sediment was filtered away from the seawater, dried at 60 °C for 3–7 d and weighed. Sedimentation rates (grams of sediment per day) were calculated by dividing the dry weight of the sediment by the number of days the trap had been in the water.

Twenty years of seawater temperature data was downloaded from the NOAA buoy 1,612,480 Mokuoloe in Hawai'i. Monthly maximum and minimum temperatures were calculated from the data to characterize the range of temperature fluctuations that occur in Kāne'ohe Bay over 20 yr, from 1994 to 2014.

Nutrient concentrations in seawater were measured in 29 samples per reef at reefs 45, 42, 25 and HIMB at 2-week time intervals (although some of these samples could not be analyzed due to budget constraints) from November 4, 2014, to January 21, 2016. Seawater samples were collected from the surface, and 100 ml was filtered through a Whatman GC/GF filter (0.7 μm;#1825025) into an acid-washed plastic bottle that had been rinsed four times with the filtered water from that site that day. The seawater samples were immediately placed on ice until they were returned to the laboratory and frozen in a − 20 °C freezer. Samples for each reef and time point were quantified for inorganic nutrient analysis which included silicate, phosphate, nitrite and nitrate and ammonia at the SOEST Laboratory for Analytical Biogeochemistry at the University of Hawai'i at Manoa. Data were analyzed with a one-way ANOVA to determine whether the concentrations of each inorganic nutrient varied among the reefs.

Community-scale extent of bleaching

Percent bleaching was assessed with five replicate 10 m long video transects on reef 44, reef 25 and the north side of HIMB. The video was taken on October 23, 2014, at 2 m and October 30, 2014, at 0.5 m depth, and for 2015, all transects were recorded on October 22. Each transect was at least 10 m away from the previous transect parallel to the reef crest. All of the transects were recorded by the first author, and the video recorder was held 40 cm above the benthos. Ten still frames of approximately 0.6 m^2 were extracted from each replicate video. Five of these still frames were selected at random (random numbers generated in excel) for analysis using Coral Point Count with Excel (CPCE v4.1). Fifty random points were overlaid and categorized on each still image. All of the images were analyzed by the first author, and each point that fell on a coral was characterized as bleached, partially bleached or dark. The mean percent of coral cover, percent severely bleached and percent pale were calculated as the mean from each of the five replicate transects for each depth at each reef. Differences in proportion of bleached coral

between depths (2 m and 0.5 m), between years (2014 and 2015) and among reefs (44, 25, HIMB) were tested with a three-way ANOVA of proportion severely bleached data that were normally distributed and had equal variances after an arcsine square-root transformation. This statistical analysis was conducted in SigmaPlot 12.3.

Among species bleaching susceptibility

Thirty-minute timed swims were used to assess the bleaching susceptibility of different coral species in Kāne'ohe Bay. During each swim, the first author only swam in one direction, and he was careful not to survey the same reef region more than once. Nine patch reefs (44, 43, 42, 25, 22, 20, 5, 3, north side of HIMB) were surveyed on October 29, 2014, to November 6, 2014, and October 19, 2015, to October 22, 2015, at depths between 0 and 7 m, and every individual coral colony encountered was counted and categorized as bleached (> 90% bleached or very pale) or healthy. The proportion bleached was calculated as the number of individual colonies bleached divided by the total number of colonies counted for each site. The percent bleached was calculated for each species on each reef, and the data shown are the means calculated from replicate reefs, with n reefs the number of reefs on which that species was found. If a coral species was found on less than three reefs, it was not included in the data analysis. For bleaching susceptibility in *Porites compressa* and *Montipora capitata*, the number of bleached or healthy colonies was counted from the five replicate video transects at 2 m and 0.5 m described above. Due to the high coral cover of *P. compressa* and *M. capitata*, only the data from three reefs (44, 25 and north side of HIMB) were used to calculate susceptibility for these two species. The data (percent of colonies severely bleached) were rank-transformed because they did not meet the assumptions of normality or equal variances. A two-way ANOVA was used to compare among species and between 2014 and 2015. A post hoc Tukeys HSD test was run in SigmaPlot 12.3 to determine groups with significantly different means.

Individual colony-scale bleaching, recovery and mortality

One hundred and forty-eight individual coral colonies were tagged and assessed for bleaching recovery and partial to full mortality from October 2014 to March 2016. At each reef, 20 individual *P. compressa* and *M. capitata* were tagged on October 24, 2014. The corals were tagged as adjacent pairs, where one colony was bleached and the other was dark brown (Fig. 2). In addition, 9–10 colonies of bleached *Pocillopora damicornis* were tagged at each reef. Since there was such a high rate of bleaching in *P.*

Fig. 2 A photograph of the paired coral colonies from October 2014. **a**. A tagged pair of *Montipora capitata* colonies and **b**. a tagged pair of *Porites compressa* colonies
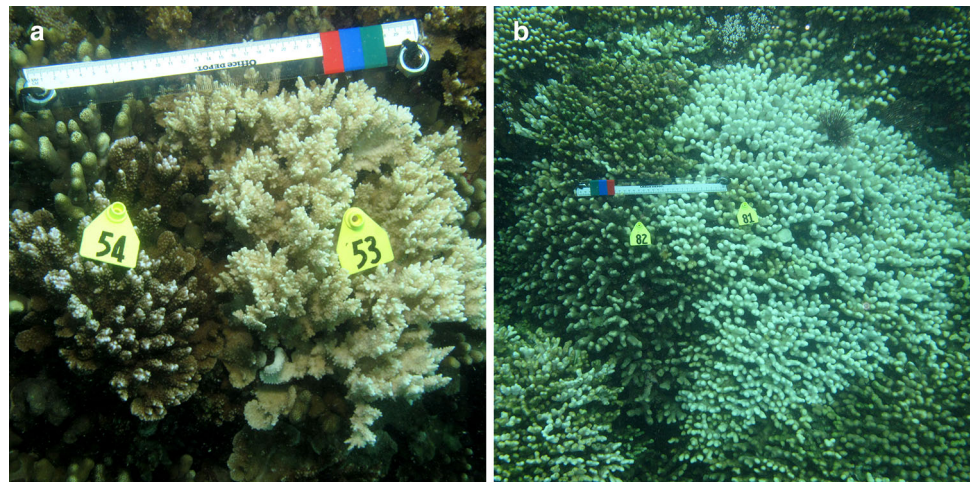
damicornis, adjacent pairs were not available. Tagged colonies were photographed every 3–6 weeks, and for each time point, the colonies were ranked with a visual bleaching score, similar to the scoring scheme used in Guest et al. (2016). A score of 0 was used to indicate a dead colony. A score of 1 was assigned to any coral that was severely bleached (greater than 90 percent of the colony area bleached or extremely pale). A score of 2 was assigned to a coral that was partially bleached or appeared pale compared to a normal color for that colony. ("Normal" colony color was determined from photographs of that individual during the March or April time point in 2015.) A score of 3 was assigned to any coral that had a dark brown color that was "normal." We confirmed that these visual scores corresponded to the relative abundance of Symbiodiniaceae in the tagged *Montipora capitata* colonies with data from a previous publication (Cunning et al. 2016). Using only the corals that bleached at each reef ($n = 10$ for all three species), the mean bleaching scores were calculated for each species at each reef at each time point. To assess for a difference in recovery rates, a three-way repeated measures ANOVA was performed with species, reef and time as fixed factors and the bleaching score as the dependent variable. In January and February 2015 an unusual windstorm toppled some colonies, changing the number of bleached corals used to calculate mean bleaching scores: reef 44 *M. capitata* $n = 9$, *P. compressa* $n = 10$ and *P. damicornis* $n = 9$; reef 25 *M. capitata* $n = 9$, *P. compressa* $n = 10$ and *P. damicornis* $n = 10$; HIMB, *M. capitata* $n = 7$, *P. compressa* $n = 8$ and *P. damicornis* $n = 8$.

No partial mortality was observed in May 2015, so photographs of individual colonies at March 31, 2016, were assessed for mortality analysis and the frequency of the number of colonies experiencing full, partial and no mortality was compared among species and among reefs using a Chi-squared test.

Results

Long-term seawater temperature data

From 1994 to 2014 seawater temperatures in Kāneʻohe Bay fluctuated from a maximum of 31.4 °C to a minimum of 19 °C, with temperatures above 30 °C only in 1996 and 2014 (Fig. 3a). A comparison of seawater temperatures in Kāneʻohe Bay during June–December in 2014 and 2015 shows that the corals were exposed to different thermal regimes with similar thermal maxima, and both years resulted in extensive bleaching in Kāneʻohe Bay (Fig. 3b). In 2014, there were 6 days where the mean temperature was 30 °C and above, and in 2015, there were 17 days of 30 °C and above. In the main Hawaiian Islands, there were differences in the number of degree heating weeks (DHW) with 6 DHW (°C week) in 2014 and 12 DHW (°C week) in 2015. In 2014, the maximum bleaching threat was an alert level 1 during the month of October, but in 2015, there was an alert level 1 in September and an alert level 2 in October (NOAA 2015).

Community-scale extent of bleaching

In both 2014 and 2015, there was more than 67% coral cover that was bleached and pale (both categories combined) in the shallow waters of Kāneʻohe Bay. The area surveyed for bleaching in video transects for Kāneʻohe Bay was assessed in both 2014 and 2015 at two different depths (0.5 m and 2 m; Table 1) using a total of 150 still photographs taken from the video data. The data for proportion of coral cover severely bleached showed no difference among the reefs (three-way ANOVA, $F = 0.408$, $p = 0.667$), but there was significantly less bleaching at 2 m depth compared to 0.5 m ($F = 29.379$, $p < 0.001$). There was significantly less bleaching in 2015 compared to 2014 ($F = 6.608$, $p = 0.013$). There was only one
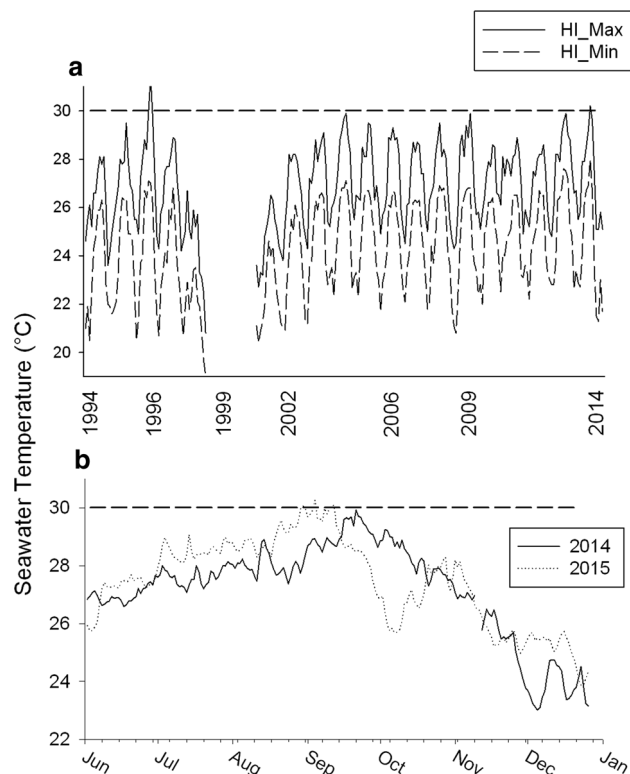
Fig. 3 Seawater temperature profiles. Temperature data were downloaded from NOAA buoys as described in the methods. **a** The temperature variation at Kāne'ohe Bay during 20 yr. The seawater temperature maximum (solid line) and the temperature minimum (dotted line) for Kāne'ohe Bay, Hawai'i. **b** Kāne'ohe Bay seawater temperature comparison of 2014 (solid line) and 2015 (dotted line) from June to January

significant interaction between year and reef (F = 3.307, $p = 0.045$) that showed reef 25 in 2015 had less bleached coral cover than in 2014.

Among species bleaching susceptibility

Susceptibilities to bleaching varied among coral species in Kāne'ohe Bay (Table 2). There was a significant difference in the proportion of severely bleached colonies among coral species (two-way ANOVA, $F_{7,82} = 27.400$, $p < 0.001$). A Tukeys HSD post hoc test showed that *Pocillopora* spp. were the most susceptible and *Leptastrea purpurea* the least. There were significantly fewer colonies bleached in 2015 compared to 2014 ($F_{1,82} = 12.787$, $p < 0.001$). There was no interaction between coral species and year ($F_{7,82} = 1.088$, $p = 0.378$).

Individual colony-scale bleaching, recovery and mortality

The individually tagged corals showed different rates of visual recovery from bleaching among species, with *P. compressa* recovering faster than *M. capitata* and *P. damicornis* (Fig. 4, three-way RM ANOVA, $F_{2,76} = 5.982$, $p = 0.004$). There was no difference in the rate of recovery among the three reefs (three-way RM ANOVA, $F_{2,76} = 1.156$, $p = 0.321$). There was an interaction between reef and time ($F_{38,76} = 1.621$, $p = 0.010$), with *M. capitata* showing reduced recovery at HIMB for one time

Table 1 The extent of bleaching on three reefs in Kāne'ohe Bay, O'ahu, Hawai'i.

Reef	Year	Depth (m)	% Coral cover (SE)	% Bleached (SE)	% Pale (SE)
HIMB	2014	0.5	60.1 (3.4)	22.9 (5.1)	62.1 (4.6)
		2	56.2 (5.9)	12.3 (3.3)	45.6 (2.8)
	2015	0.5	61.6 (2.9)	27.5 (8.5)	45.2 (5.8)
		2	51.3 (4.3)	13.0 (3.9)	31.7 (5.1)
25	2014	0.5	72.0 (4.2)	36.3 (4.2)	56.1 (5.1)
		2	85.0 (3.0)	17.1 (4.6)	55.7 (7.6)
	2015	0.5	72.4 (7.1)	17.5 (4.7)	49.8 (3.1)
		2	85.4 (2.5)	6.9 (0.5)	35.7 (5.3)
44	2014	0.5	54.7 (4.6)	25.0 (4.9)	57.7 (5.0)
		2	78.1 (3.0)	14.8 (3.1)	58.5 (4.0)
	2015	0.5	47.7 (3.2)	22.5 (5.8)	45.7 (6.4)
		2	76.8 (3.8)	4.9 (1.2)	39.5 (4.1)

Bleaching is defined as points that were pure white, and paling is defined as brown but paler than a normal brown. % Bleached and % pale were calculated as a proportion of total coral cover.

$n = 5$ for each reef at each depth in both years. A three-way ANOVA showed significantly more bleaching at 0.5 m than 2 meters ($p < 0.001$), significantly more bleaching in 2014 than 2015 ($p = 0.013$), but no difference among the reefs ($p = 0.667$)

Table 2 The bleaching susceptibility of different coral species in Kāneʻohe Bay, Oʻahu, Hawaiʻi.

Coral species	Year	% Bleached (SE)	n reefs	# of colonies
Pocillopora meandrina[a]	2014	100 (0)	4	7
	2015	100 (0)	4	8
Pocillopora damicornis[a]	2014	90.6 (2.4)	9	1518
	2015	81.4 (7.6)	9	1177
Montipora spp.[b]	2014	65.3 (7.1)	8	161
	2015	44.3 (10.8)	7	146
Pavona varians[b]	2014	62.9 (13.8)	4	36
	2015	24.9 (9.2)	7	41
Porites compressa[b]	2014	43.7 (2.6)	3	903
	2015	19.7 (0.7)	3	980
Montipora capitata[bc]	2014	36.7 (1.9)	3	338
	2015	16.6 (4.7)	3	388
Fungia scutaria[b]	2014	35.4 (4.0)	9	662
	2015	26.5 (10.7)	9	584
Leptastrea purpurea[c]	2014	0.75 (0.8)	7	563
	2015	0 (0)	6	823

Susceptibility was calculated based on proportion of individual bleached colonies per patch reef. Mean was calculated from replicate reefs (n).

A two-way ANOVA showed there was significantly more bleaching in 2014 compared to 2015 ($p < 0.001$) and significantly different susceptibility among species ($p < 0.001$); the superscript letters next to species names indicate significant groupings as determined by a Tukey's post hoc test

point, December 17, 2015. There was also a significant interaction between species and time ($F_{38,76} = 3.966$, $p < 0.001$).

Overall, there was 7.5% full mortality of tagged colonies, with 5 (10%) *M. capitata* (three bleached and two healthy colonies) and 5 (19%) *P. damicornis*, but no colonies of *P. compressa* that died during the monitoring (Fig. 5). The frequency of colonies experiencing full and partial mortality varied among species with similar rates in *P. damicornis* and *M. capitata* but lower rates of mortality in *P. compressa* (Fig. 5, Chi-squared = 14.416, $p = 0.006$). The mortality rate was similar at HIMB (7.9%), at reef 25 (6.3%) and at reef 44 (8.5%). Mortality was not significantly different among reefs (Chi-squared = 9.242, $p = 0.055$), although the power was low on this analysis.

Reef-scale environmental data

The 2014 and 2015 data for temperature (Ritson-Williams and Gates 2016a), sediment (Ritson-Williams and Gates 2016b), light (Ritson-Williams and Gates 2016c) and inorganic nutrients (Ritson-Williams et al. 2019) at each reef are downloadable datasets archived at Zenodo. The temperatures from October 2014 to December 2015 at the three reefs were statistically different using a least square means analysis in R (Supplemental Figure 1). The mean temperature for the reef at HIMB was 26.0 °C, which was significantly different than 26.1 °C at reef 25 ($p = 0.001$), and HIMB was different from the mean of 26.1 °C at reef 44 ($p = 0.004$). However, it is important to note that this analysis detected a difference of temperatures of 0.1 °C, which is probably a type I error due to the high number of samples, and 0.1 °C is smaller than the error that is associated with the HOBO loggers' ability to detect temperature. From June to December, temperatures ranged from 23.0 to 30.0 °C in 2014 and from 23.9 to 30.3 °C in 2015 (Fig. 3b). In 2014, seawater temperature means were at or above 30 °C for 6 days, and in 2015, they were at or above 30 °C for 17 days. PAR was converted to daily light integrals, and at the reef at HIMB, there was a minimum of 1311 mol/m^2/day and a maximum of 35,632 mol/m^2/day, at reef 25 the minimum was 1132 mol/m^2/day and the maximum was 34,119 mol/m^2/day, and at reef 44 the minimum was 559 mol/m^2/day and the maximum was 33,277 mol/m^2/day. Using a least squares means approach, there were significant differences in the mean daily light integral between reefs, with 21% more light at the reef at HIMB than reef 25 ($p < 0.001$), 13% more light at the reef at HIMB than at reef 44 ($p < 0.001$) and 9% more light at reef 44 than at reef 25 ($p < 0.001$) (Supplemental Figure 2). Sediment load at each reef was variable over time during the monitoring period (Supplemental Figure 3), but not significantly different among reefs (one-way ANOVA, $F_{2,33} = 2.992$, $p = 0.064$). Sediment rates ranged from a minimum of 0.016 g/day to a maximum of 0.158 g/day. Over the monitoring period, there was a mean of 0.052 g/day at reef 44, 0.033 g/day at reef 25 and 0.060 g/day at HIMB. Concentrations of some inorganic
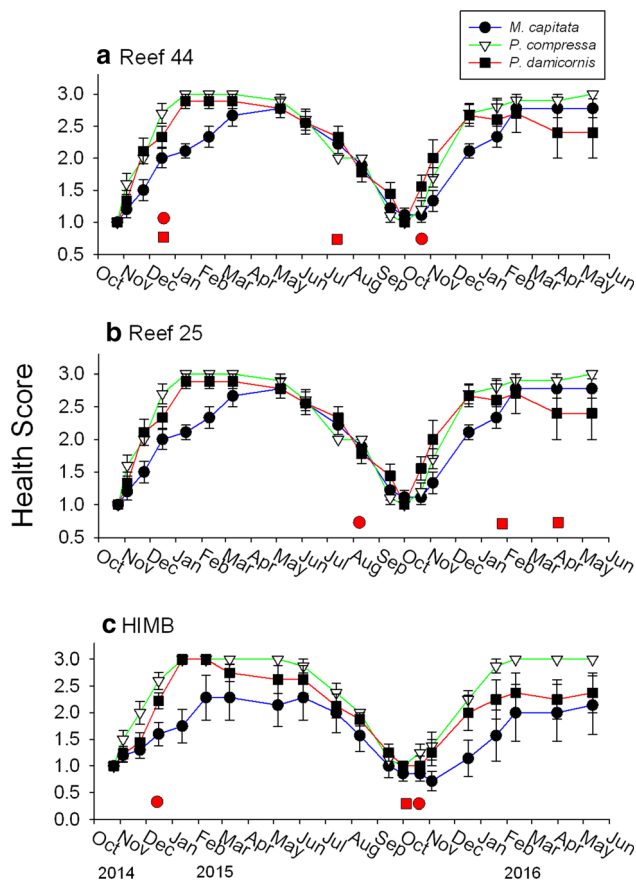
Fig. 4 Coral condition in three species of corals: *Montipora capitata* (white triangles), *Porites compressa* (circles) and *Pocillopora damicornis* (squares). Only bleached colonies from the pairs are used to calculate the means that are represented by the symbols at each time point with error bars representing ± 1 SE. Bleaching was assessed visually with a score of 0 (dead), 1 (severely white), 2 (partially bleached or pale), 3 (darkly pigmented). **a** Reef 44 **b** reef 25, C. north side of Hawai'i Institute of Marine Biology. The red symbols at the bottom of the figure represent individual mortality events for a single coral colony. For the rates of recovery, there was no statistical difference among sites, but there was significantly faster recovery in *P. compressa* compared to *M. capitata* and *P. damicornis* ($p = 0.004$)

nutrients were significantly different among the reefs from 2014 to 2016 as determined by a one-way ANOVA (phosphate $F_{2,84} = 7.491$, $p = 0.001$; ammonia $F_{2,84} = 5.054$, $p = 0.008$; nitrate and nitrite $F_{2,84} = 13.620$, $p < 0.001$) There was no difference in the concentrations of silicate among the reefs (Supplemental Figure 4; $F_{2,84} = 1.735$, $p = 0.183$).

Discussion

The corals in Hawai'i experienced two successive summers of high seawater temperatures that resulted in extensive coral bleaching, but in Kāne'ohe Bay, there was very little mortality after these events. Some coral colonies such as
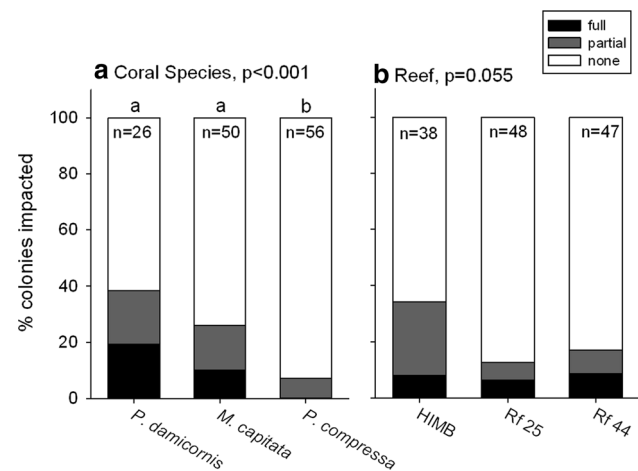
Fig. 5 The frequency of mortality in coral colonies in March 2016 following two successive bleaching events. **a** Coral species, *Pocillopora damicornis*, *Montipora capitata* and *Porites compressa*. **b** Patch reefs in Kāne'ohe Bay, reef 44 is in the northern section of the bay, reef 25 is in the middle and the reef at the Hawai'i Institute of Marine Biology is in the southern portion of the bay. Bars represent the relative frequency of a type of mortality, with the open bar representing no mortality, the gray bar representing partial mortality and the black bar representing the full mortality of an individual colony. *n* is the total number of colonies that were used to calculate frequency within each bar

the tagged colonies that resisted bleaching never fully bleached in either event. Bleaching transects in Kāne'ohe Bay showed that both years had extensive bleaching, impacting 60–80% of the coral cover. However, most of the corals in Kāne'ohe Bay recovered from both bleaching events and cumulative mortality was less than 10%. The extent of a temperature anomaly and its duration are critical variables for the severity of coral bleaching (Glynn et al. 2001; McClanahan et al. 2007). In both 2014 and 2015, there was a peak in seawater temperature during September above 30 °C, but in 2015, the thermal stress started earlier and resulted in longer cumulative thermal stress (12 DHW in 2015 compared to 6 DHW in 2014). In October and November, the seawater temperatures dropped rapidly, possibly contributing to the high rates of survival and recovery in the corals in Kāne'ohe Bay (Fig. 4). Coral bleaching has previously only occurred in 1996 in the main Hawaiian Islands, the only other year on record when seawater temperatures peaked above 30 °C. Many other sites throughout the Pacific and Indian Oceans experienced extensive coral mortality during the mass bleaching from 2014 to 2016 (Hughes et al. 2017; Burt et al. 2019; Head et al. 2019; Raymundo et al. 2019; Vargas-Angel et al. 2019). However, some sites such as the Galapagos (Riegl et al. 2019), North Western Australia (Richards et al. 2019), and our data from Kāne'ohe Bay, show relatively little coral mortality associated with this extensive thermal stress. Due to the resistance of some genotypes of coral to

thermal stress and the rapid recovery of these populations of corals, we argue that these reefs in Hawai'i are resilient to these episodes of thermal stress. While frequency, severity and extent of coral bleaching are increasing across the planet, projecting long-term trajectories of coral populations should include data from those coral populations that might be able to resist thermal stress.

There were different rates of susceptibility to bleaching among different coral species. These rates of susceptibility for Hawaiian coral species match published species susceptibilities from other locations (Marshall and Baird 2000). However, the data show that *Pocillopora spp.* were especially vulnerable to high seawater temperatures in both summers. Of the coral species in which individual colonies were monitored, *P. damicornis* had the highest mortality. There were very low rates of bleaching in the encrusting *Leptastrea purpurea*. This small encrusting species had a bleaching susceptibility of less than 1% both years of study. Importantly, we collected these data as close to the maximum seawater temperature as possible. However, due to the inherent uncertainty about when it was the "maximum seawater temperature" in situ, comparing these surveys between 2 years might be impacted by the timing of the surveys, but in all cases, we surveyed the corals for maximum bleaching before we saw any signs of recovery in the community. The fact that some species will be winners and others will be losers (Loya et al. 2001; Edmunds et al. 2014) is critical data for predicting the impact of future thermal stress on species diversity in reef communities.

The among species susceptibility data suggest that the reefs in Kāne'ohe Bay are becoming increasingly resistant to thermal stress events since there were significantly less colonies affected by bleaching in 2015 than in 2014. However, this data could be biased by different duration of thermal stress since there were temperatures above 28 °C in June 2015 but not until August 2014. Some research shows that corals are more likely to resist bleaching if they are exposed to a longer duration of warm temperatures prior to thermal stress (Ainsworth et al. 2016), which corresponds to the seawater temperature pattern in 2015. However, all of the tagged colonies that bleached in 2014 bleached again in 2015, suggesting that these individual corals did not acclimatize to thermal stress. Monitoring at the individual scale gives us a powerful tool to tease apart how reefs are adapting to thermal stress, are individuals dying leaving only the resistant individuals alive or are individuals acclimatizing allowing the preservation of genotypic diversity through a bleaching event. So far, the tagged corals in Kāne'ohe Bay do not show any signs of acclimatization to thermal stress; however, the physiology of these corals is still being studied.

Overall, the 148 individual coral colonies that we monitored showed high variability in bleaching susceptibility, but the tagged *Montipora capitata* colonies that did bleach showed consistent recovery of their symbionts (Cunning et al. 2016). The paired corals monitored in this study are not a random sampling of *P. compressa* or *M. capitata*. These colonies were intentionally selected as pairs to minimize the potential confounding effects of microhabitat heterogeneity. However, these pairs were not an anomaly, and there were bleached and unbleached corals adjacent to each other at every reef visited, indicating high phenotypic diversity within this population.

In situ recovery rates were relatively rapid with most corals becoming darkly pigmented 3 months after experiencing maximum seawater temperatures (Fig. 4). In a related publication that also used some of these same pairs of *M. capitata* and *P. compressa*, the two species were found to use different energy resources during recovery from bleaching. But there was no clear physiological difference between the bleaching susceptible or resistant phenotypes within a species (Wall et al. 2019). In 2014 and 2015, these same tagged *M. capitata* colonies were tracked for their *Symbiodiniaceae* abundance and the health scores reported here corresponded very well to quantification of the abundance of *Symbiodiniaceae* cells normalized to host coral cells (Cunning et al. 2016). However, while Cunning et al. (2016) report a slower recovery of corals at HIMB, there was no difference in the recovery rate among reefs detected in the current study. This is probably due to reduced resolution using the visual scores. The visual scores were used because they are nondestructive sampling technique and these methods allowed a more frequent monitoring than is found in most studies.

In 15 months, only five *Montipora capitata* and five *Pocillopora damicornis* individual colonies died. There was no partial mortality after the 2014 bleaching, but there was some after the bleaching in 2015, probably due to the cumulative effect of consecutive stress events. Since partial mortality does not eliminate a genotype from the population, this impacts coral cover but not genotypic diversity. These low rates of mortality are probably due to relatively rapid rates of seawater cooling in November of both 2014 and 2015 (Fig. 3b). Kāne'ohe Bay also has relatively high rates of sedimentation compared to other reefs in Hawai'i, and reefs that have low light stress and high potential for heterotrophic nutrition are probably more capable of recovery after a bleaching event (Guest et al. 2016).

There was variation in bleaching susceptibility among species and also within species. Some studies have found that hosting different Symbiodiniaceae types can contribute to variation in bleaching susceptibility (Rowan et al. 1997; Glynn et al. 2001; Jones et al. 2008; Cunning et al. 2015). However, analysis of Symbiodiniaceae in these tagged *M.*

capitata colonies in Kāne'ohe Bay showed that while colonies hosting type D1a did not bleach, only some colonies hosting C31 bleached, while other colonies did not (Cunning et al. 2016). Furthermore, *Porites compressa* in Hawai'i is only known to host ITS2 type C15 (LaJeunesse et al. 2004; Stat et al. 2013), suggesting that intraspecific bleaching resistance is not driven by Symbiodiniaceae type. There are many other potential factors that contribute to variation in intraspecific phenotypes, and further work on coral genetic adaptation (Palumbi et al. 2014), gene expression and physiology (Csaszar et al. 2009; Barshis et al. 2013) and microbiome (Ainsworth et al. 2010; Littman et al. 2011; Bourne et al. 2016; Ziegler et al. 2017; Rosado et al. 2019) is ongoing. Regardless of the cause, these field surveys document that within species variation in populations is an important resource for adaptation to climate change.

Local adaptation is one mechanism that has been studied in terrestrial environments that allows plants to survive in degraded habitats (Joshi et al. 2001; Siol et al. 2010; Anderson et al. 2011). Local adaptation to stressful conditions is well documented, but has only recently been studied for corals (Palumbi et al. 2014) and Symbiodiniaceae (D'Angelo et al. 2015). Local adaptation may be driving the resilience of Kāne'ohe Bay corals because these corals have been exposed to annual temperature variations greater than 10 °C (Fig. 2) and Kāne'ohe Bay has a long history of human disturbance (Bahr et al. 2015). In an experimental comparison between corals of Kāne'ohe Bay and those collected from Waimanalo Bay, the colonies from Kāne'ohe Bay were less susceptible to elevated seawater temperatures and ocean acidification treatments (Jury and Toonen 2019). Currently, *P. compressa* and *M. capitata* make up greater than 95% of the coral cover on in Kāne'ohe Bay's reefs and reduced species diversity can be found in other disturbed habitats, which may be an important consequence of local adaptation. Climate change is known to lower genotypic diversity through multiple mechanisms (Pauls et al. 2013), and thermal stress can reduce genetic diversity on reefs (Selkoe et al. 2016).

Resilience has been attributed to a few "refuge" or "oases" reefs in the Pacific (Cacciapaglia and van Woesik 2015; Guest et al. 2016, 2018; Richards et al. 2019; Riegl et al. 2019), but the response of corals to thermal stress in these refuge habitats is quite variable. Corals in French Polynesia were assessed for bleaching susceptibility during four bleaching episodes from 1991 to 2007 (Pratchett et al. 2013). While the trends show increased resistance, since these authors did not monitor the same colonies it is impossible to tell if this is a result of acclimatization, differential mortality or an artifact of different environmental stressors during different bleaching events. Macroscale refugia have been predicted for multiple locations in the Pacific and Indian Oceans, but there is relatively little known about phenotypic variation within these refugia populations (Cacciapaglia and van Woesik 2015). In 2010, the reefs in Singapore were characterized by relatively low rates of bleaching and rapid recovery within a few months (Guest et al. 2016). Corals in nearshore bays of Palau were more resistant to bleaching than offshore reefs even though they had higher seawater temperatures (van Woesik et al. 2012). Sites in Africa showed less bleaching-associated mortality if they experience the largest temperature variation (McClanahan et al. 2007). The reefs at Singapore and Palau are characterized by highly variable temperature regimes and high sedimentation and so are the reefs in Kāne'ohe Bay. Meta-analyses of bleaching susceptibility suggests that reefs exposed to a wide fluctuation of annual seawater temperatures might be more resilient to thermal stress (Safaie et al. 2018; McClanahan et al. 2019). Additionally, these reefs have a reduced coral diversity compared to other nearby reefs. Using these case studies, there is a trend for corals living in fluctuating temperatures and high turbidity to be more resistant to coral bleaching even though they live in "degraded" conditions. This suggests that corals adapted to local stress may be more resilient in the face of climate change, which is critical information for identifying other sites that might provide refugia from bleaching.

The two successive bleaching events in Hawai'i in 2014 and 2015 were unprecedented, and the corals monitored here show that some colonies and reefs can recover from two consecutive thermal stress events. Rarely are multiple scales of coral reefs monitored for their resistance to and recovery from bleaching, but it is critical that researchers integrate across scales to identify the features of coral resilience. No one monitoring protocol is perfect, but a standardized approach that includes surveys at multiple spatial scales can better assess coral resilience to fully understand which coral populations might persist in a future of climate change. By studying extreme coral reefs, we can identify populations of corals that can resist and recover from thermal stress.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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