



NOTE

Autumn coral bleaching in Hawai'i

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ABSTRACT: Coral bleaching in Hawai'i was first reported in 1996 and subsequently occurred in 2014 and 2015. These largely summer events did not persist past November. In autumn 2019, Hawai'i experienced persistent warm water until December, resulting in bleaching of many pocilloporid coral colonies, particularly *Pocillopora meandrina*. We followed the fates of 357 adult *P. meandrina* and 377 juvenile *Pocillopora* spp. off Waikiki on the south shore of O'ahu. Water temperatures at 5–18 m depth at this site consistently remained above a bleaching threshold of 28°C from September until mid-December. For adult colonies, 96% bleached at least partially, 4% bleached fully, and 11% died by March. Among juvenile colonies, 21% bleached, of which 47% died by March 2020. While mortality was low compared to previous bleaching events in Hawai'i, such protracted bleaching late into the autumn increases the annual period of temperature stress, which may not bode well for the future of Hawaiian and other high-latitude coral reefs.

KEY WORDS: Coral bleaching · *Pocillopora* · Hawai'i

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1. INTRODUCTION

As oceans inexorably warm, corals in Hawai'i are predicted to bleach every year by the middle of this century (van Hooidonk et al. 2016). The 2019 bleaching event in Hawai'i persisted later in the year than all past events (Jokiel & Brown 2004, Bahr et al. 2015, 2017, Rodgers et al. 2017), which lends credence to this dire prediction.

Coral bleaching occurs when stressors, such as elevated water temperatures, cause coral colonies to expel their algal symbionts (Symbiodiniaceae), making the colony appear white or 'bleached' (Brown 1997, Fitt et al. 2001). Globally, bleaching events have become more frequent, widespread, and severe (Oliver et al. 2009, Hughes et al. 2018). Hawai'i was once thought to be a refuge from heat-related stress because of its location further north than other tropical reefs (Jokiel & Brown 2004), although this is no longer true. Coral bleaching in the Main Hawaiian Islands (MHI) was first documented in 1996, followed by events in 2014 and 2015 (Jokiel & Brown 2004,

Bahr et al. 2015, Cunning et al. 2016, Rodgers et al. 2017).

Widespread bleaching is expected in Hawai'i when anomalously warm water surpasses 28°C (Jokiel & Brown 2004), with longer periods of elevated temperatures leading to greater bleaching severity. Severe bleaching events can cause coral mortality, resulting in the loss of valuable habitat structure that can disrupt community assemblages of coral-associated species (Booth & Beretta 2002, Garpe et al. 2006). The severe bleaching event of 2015 is one such example, which led to a loss of nearly half of the live coral cover on the leeward coast of the island of Hawai'i, including 78% of *Pocillopora meandrina* colonies (Kramer et al. 2016). Past bleaching events in Hawai'i, such as in 2015, occurred between late August and October, when ocean temperatures are typically highest. Repopulation of algal symbionts was well underway by mid-November to early December after temperatures had normalized, with coral colonies regaining most of their color (Jokiel & Brown 2004, Bahr et al. 2015, Rodgers et al. 2017, Ritson-Williams & Gates 2020).

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Here, we document the unusual timing of an autumn bleaching event, rate of response, and extent of bleaching for pocilloporid corals on a spur-and-groove reef off Waikīkī Beach on the south shore of O'ahu before, during, and following the peak of bleaching in the summer and fall of 2019. We focused on numerically dominant adult *P. meandrina* and juvenile *Pocillopora* spp. Pocilloporid corals form highly complex branching colonies, are commonly found on shallow reefs with high water motion, and have historically exhibited a strong bleaching response to elevated water temperatures (Jokiel & Brown 2004, McClanahan et al. 2020, Ritson-Williams & Gates 2020, Burgess et al. 2021). While initial reports indicated bleaching in 2019 was less severe than previous bleaching events for the MHI (Winston et al. 2020), the protracted duration and late timing of this event are unique and foreboding for Hawai'i and other high-latitude coral reefs.

2. MATERIALS AND METHODS

2.1. Study site

Our study site was located 800 m offshore of Waikīkī Beach on the south shore of O'ahu, Hawai'i (21° 16' 10" N, 157° 50' 15" W) ranging from 5 to 18 m in depth (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m675p199_supp.pdf). The total area of the study site was approximately 10 ha and included mostly spur-and-groove reef and sandy bottom. Surveyed adult colonies were located on hard substrate, whereas the juvenile corals we studied had settled naturally to 6 pre-existing 1 m³ concrete settlement modules located in sand flats 33 m from natural reef (see Hixon & Beets 1993 for illustrations of modules).

2.2. Water temperature

Water temperature at the site was recorded using HOBO Pendant Temperature/Light Data Loggers ($\pm 0.53^\circ\text{C}$ accuracy; Onset Computer) placed at 12 and 18 m on the concrete settlement modules (loggers deployed May 2018) and at 5 m on the adjacent natural reef (logger deployed June 2019). Sea surface temperature and degree heating week (DHW) data were obtained from the National Oceanic and Atmospheric Association Coral Reef Watch Daily 5 km Regional Virtual Stations time series database for the MHI (<https://coralreefwatch.noaa.gov/product/5km/>; Liu et al. 2006).

2.3. Adult coral surveys

Two groups of adult *Pocillopora meandrina* colonies (>100 mm diameter) were independently tracked as parts of separate projects following associated fish communities. The first dataset followed 18 clusters of 4 closely positioned *P. meandrina* colonies ($n = 72$) occurring at 2 depths: shallow (5–8 m) and deep (11–15 m; Fig. S1). Coral colony condition was documented as normal, totally bleached, or dead (no living tissue remaining), and branch tips were characterized as normal, lightened (relative to the rest of the colony), spotted, or bleached (Fig. 1). Initial surveys were conducted in the first week of July 2019, with subsequent weekly surveys from the second week of August through the first week of October. Two additional surveys were also conducted in November and March 2020.

Simultaneously, a second project followed all adult *P. meandrina* colonies in 100 m² plots ($n = 14$) scattered throughout the study site (Fig. S1). Each colony within the plots ($n = 285$) was initially surveyed in July or early August 2019, prior to widespread bleaching, to identify all living colonies. To document bleaching, recovery, and mortality at the height of and following the bleaching event, subsequent surveys were conducted in November 2019 and March 2020.

2.4. Juvenile coral surveys

Juvenile pocilloporid data came from quarterly surveys completed as part of a field experiment using 1 m³ concrete settlement modules ($n = 6$). An initial survey of 367 juvenile *Pocillopora* spp. (<50 mm diameter; Doropoulos et al. 2015) was conducted in May 2019, prior to bleaching. Subsequent surveys documenting their status (normal, bleached, or dead; Fig. 2) were conducted in September, November, and March 2020.

3. RESULTS

3.1. Water temperature

The 28°C bleaching threshold was surpassed during brief periods in June and July 2019. Temperatures continuously remained above the bleaching threshold from 5 September through 31 October (56 d), and again from 25 November to 12 December (17 d; Fig. 3A). Between 18 June and 25

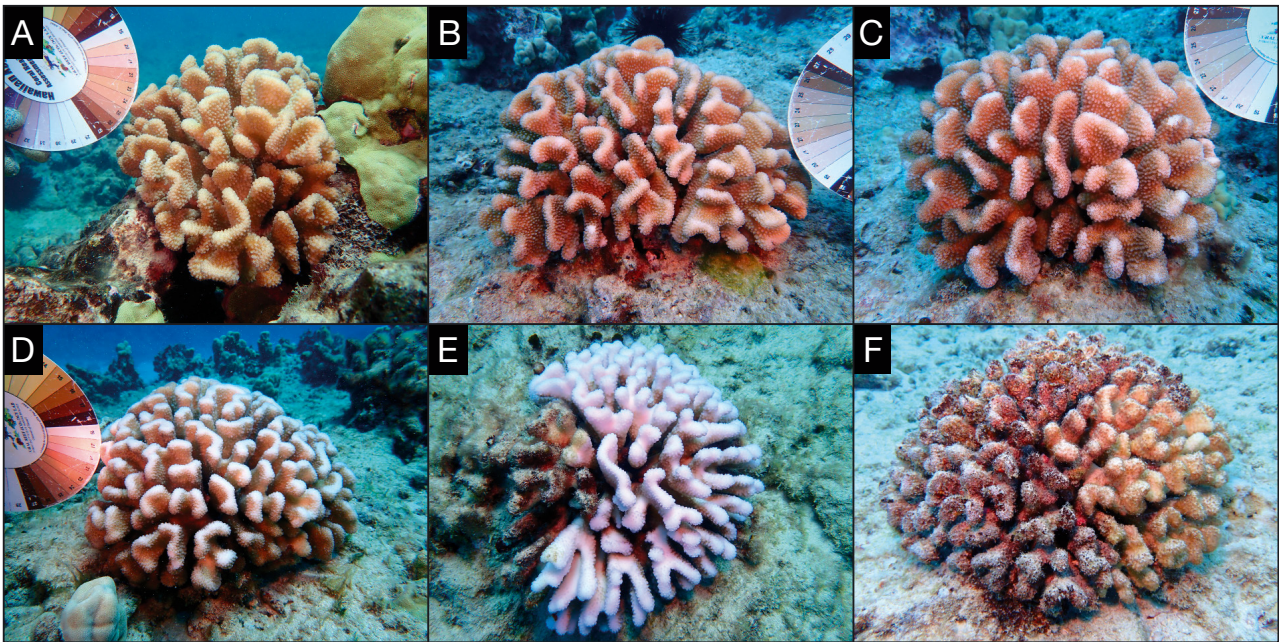


Fig. 1. Adult *Pocillopora meandrina* bleaching states: (A) normal colony hue and pigmentation, (B) lightening of the branch tips, (C) spotted branch tips, (D) bleached branch tips, and (E) colony-wide loss of color. (F) Dead portions of colonies were quickly colonized by turf and filamentous algae

December, 163 out of 191 d had maximum daily water temperatures in excess of 28°C. All 3 depths experienced a peak of at least 28.4°C for the entire day on 26 September, including a maximum of 29.4°C at the shallowest station. A secondary temperature spike of 29.4°C occurred at the deepest station on 29 November, followed shortly thereafter by a less intense spike at the 12 m station. Subsequently, water temperatures stratified by depth, with the warmest temperatures at 12 and 18 m compared to the 5 m station. The MHI experienced DHW values greater than 4, the point at which coral bleaching is expected, from 30 August to 22 December, including a period from 21 September

to 29 November where DHW remained above 8, at which point mass bleaching and the onset of coral mortality are expected (Eakin et al. 2009). The maximum value of DHW recorded was 13.6, lasting from 23 to 30 October.

3.2. Adult coral colonies

The initial sign of bleaching stress, i.e. lightened color at the branch tips (Fig. 1B), was first noted among adult colonies during the third week of August 2019 (Fig. 3B). Lightened branch tips maintained some pigment and the general hue of the

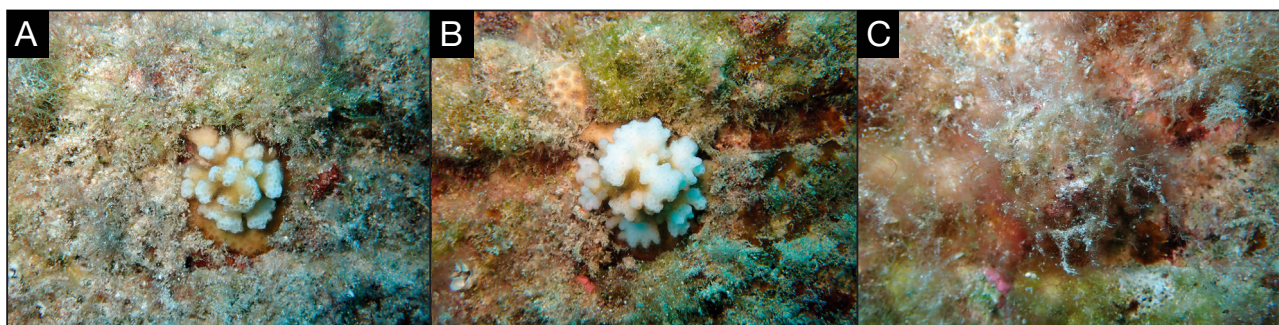


Fig. 2. Juvenile pocilloporid colony states: (A) normal, (B) uniformly bleached, and (C) dead and overgrown by turf algae

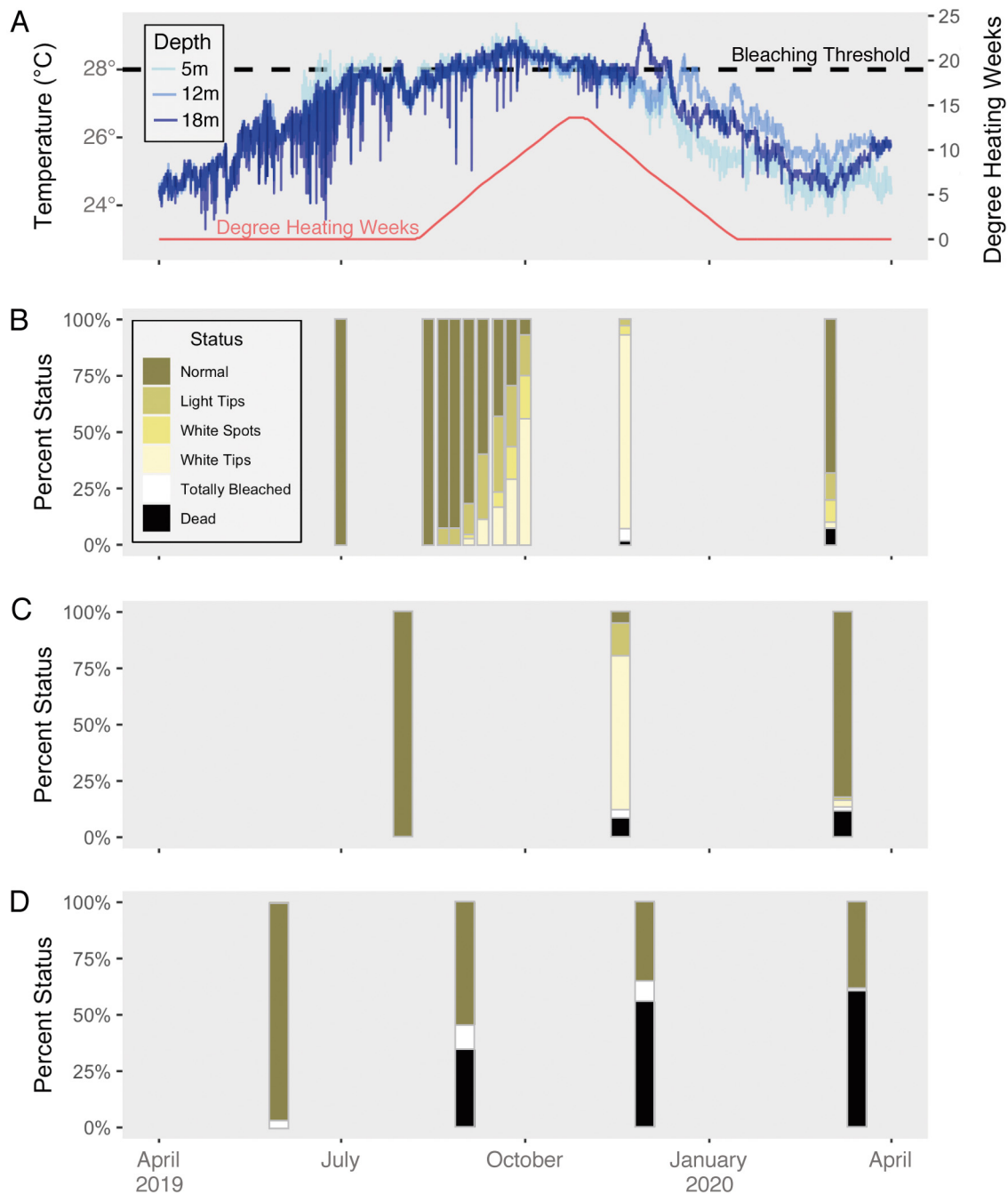


Fig. 3. Course of the 2019 coral bleaching event off Waikīkī Beach, O'ahu, Hawai'i, comparing 3 separate data sets. (A) Temperature profiles at 5, 12, and 18 m depths, measure of degree heating weeks (NOAA Coral Reef Watch), and the NOAA 28°C bleaching threshold (dashed line). (B) Status of adult *Pocillopora meandrina* in clusters (n = 72) before (July), during (August–October), and after the bleaching event (March). (C) Status of adult colonies in plots before, during, and after the bleaching event (n = 285). (D) Status of juvenile coral colonies on concrete settlement modules during annual quarterly censuses throughout the bleaching event (n = 377)

colony, though the color was less saturated. By the second week of September, some colonies exhibited more severe signs of bleaching, with either white spots (Fig. 1C) or complete bleaching (Fig. 1D) only

on the branch tips. Although total colony bleaching (Fig. 1E) was observed in only 4% of adult colonies during the bleaching peak in late November, 96% of adult colonies surveyed showed some sign of bleach-

ing stress (71.7% white branch tips, 12.3% light branch tips, 7.2% dead, 3.9% totally bleached, and 0.8% spotted branch tips). Additionally, colonies in deeper clusters exhibited signs of bleaching, on average, 6.7 d earlier than those in shallower areas (t -test, $p < 0.05$). By March 2020, 79.6% of monitored adult coral colonies had recovered normal coloration, yet 8.7% still had lightened or bleached branch tips, and 11% died (Fig. 1F). Of the 74 adult colonies in the clusters that were followed weekly, 6 died during this study (8.1%). All of these colonies exhibited bleaching of their branch tips, with 1 colony bleaching entirely. Additionally, 3 other colonies exhibited total colony bleaching during the bleaching event but had recovered to lightened or bleached branch tips by March. All colonies lost or damaged due to wave stress were excluded from analysis. Crown-of-thorns seastars *Acanthaster planci* were not observed during this study, whereas cushion stars *Culcita novaeguineae* were commonly seen throughout the study site.

3.3. Juvenile coral colonies

At the beginning of September 2019, 10.9% of all juvenile corals on the 6 settlement modules showed signs of bleaching compared to 0.8% at the same time the previous year, when water temperatures did not surpass the 28°C bleaching threshold (Fig. S2). In mid-November 2019, 9.3% of all colonies showed bleaching stress compared to 0.8% of colonies in November 2018. By March 2020, only 0.5% of colonies remained bleached and 64.6% of all colonies had died (66.8% had died the previous year). Additionally, mortality was lower for colonies that bleached (47.4%) compared to colonies that did not bleach (69.1%).

Over the course of the entire bleaching event, an average (\pm SE) of $19.7 \pm 4.0\%$ of juvenile colonies on the 6 settlement modules exhibited bleaching stress at some point in 2019 compared to just $2.4 \pm 0.9\%$ the previous year (t -test, $p < 0.05$), reflecting the higher temperature stress experienced by corals in 2019 (Fig. S2). Despite significantly higher bleaching rates in 2019, there was no difference in juvenile mortality rates between 2018 ($64.9 \pm 6.1\%$) and 2019 ($63.2 \pm 5.5\%$; t -test, $p = 0.84$).

4. DISCUSSION

Overall, 96% of 357 adult colonies of *Pocillopora meandrina* exhibited some degree of bleaching stress, although total colony bleaching (4%) and mortality (11%) were low compared to previous bleaching events in Hawai'i (Kramer et al. 2016). Mortality was presumably due to bleaching stress, but coral predators, such as cushion stars, may have also contributed to colony mortality (Glynn & Krupp 1986). Furthermore, mortality in juvenile corals was not significantly greater in 2019 than in the previous year, where widespread bleaching was not observed. This pattern follows previous findings that bleaching stress may have insignificant effects on juvenile coral mortality (Mumby 1999, Depczynski et al. 2013). The resistance of juvenile corals to bleaching may play a role in the persistence of local populations following bleaching events (Álvarez-Noriega et al. 2018). It is possible, however, that we did not capture the full extent of bleaching within this population due to the quarterly nature of our surveys, thereby underestimating the number of colonies that bleached before dying.

This bleaching event was unusual due to the protracted presence of warm water compared to previous events (Fig. 4), with water temperatures remaining above 28°C until the second week of December. This situation led to bleaching stress among corals late in the year and delayed recovery well into 2020. Past bleaching events in Hawai'i typically occurred between August and October, with recovery underway by December (Jokiel & Brown 2004, Bahr et al. 2015).

The timing and duration of bleaching events will be of greater concern as these events become more common. Bleaching typically occurs when sea tem-

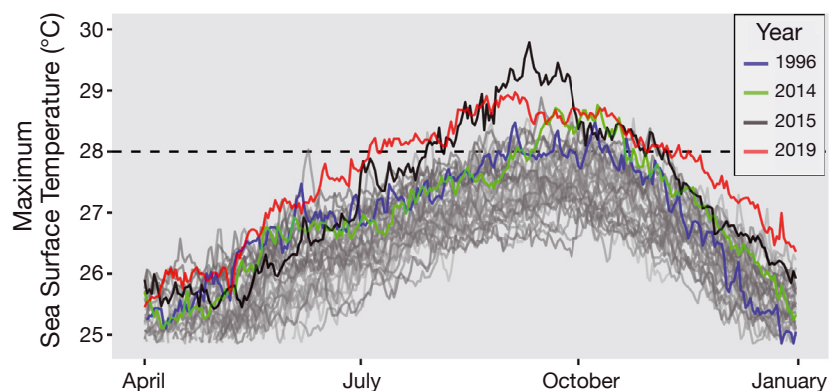


Fig. 4. Satellite-derived maximum sea surface temperatures for the Main Hawaiian Islands during the 1996, 2014, 2015, and 2019 bleaching events (NOAA Coral Reef Watch). Gray lines represent sea surface temperatures in years where coral bleaching was not documented (1985–2020)

peratures and solar irradiance are highest, pushing corals to their heat tolerance threshold (Jokiel & Coles 1990, Fitt et al. 2001). Should bleaching events become more common during autumn and winter, seasons that historically offer a refuge from thermal extremes, corals may lose the opportunity to recuperate before subsequent warming events. Additionally, bleaching stress can reduce the reproductive capabilities of corals, potentially depressing subsequent recruitment and population recovery following disturbances (Johnston et al. 2020). Alternatively, thermal stress events occurring during seasons decoupled from high solar irradiation may result in less severe bleaching responses by corals, potentially explaining the prolonged but mild bleaching we observed in 2019. Furthermore, less severe bleaching events may lead to an increase in coral thermal stress tolerance, even when whole-colony mortality is rare (Maynard et al. 2008). Regardless, with bleaching events likely to become annual occurrences (van Hooidonk et al. 2016), late and prolonged events such as this represent a new phenomenon that warrants further attention.

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