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Patterns of bleaching and recovery of *Montipora capitata* in Kāneʻohe Bay, Hawaiʻi, USA

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ABSTRACT: As ocean warming causes more frequent and severe coral bleaching worldwide, it is critical to identify biotic and abiotic factors that promote bleaching resistance and recovery. In October 2014, many colonies of the key reef-building coral *Montipora capitata* in Kāneʻohe Bay, Oʻahu, Hawaiʻi, USA, were severely bleached, while others appeared unaffected. To elucidate the role of symbiotic algae in these contrasting responses and study subsequent patterns of recovery, we tracked abundances (symbiont to host cell ratios) of clade C and D *Symbiodinium* for 6 mo in 10 bleached and 10 non-bleached colonies at 3 reefs in the northern, central, and southern regions of Kāneʻohe Bay (n = 60 colonies) using quantitative PCR. Bleaching resistance was significantly associated with the dominant symbiont clade. All bleached colonies (n = 30) were dominated by clade C symbionts, while many non-bleached colonies (n = 16) were dominated by thermotolerant clade D. However, clade C *Symbiodinium* dominated 14 other colonies that did not bleach, indicating that an alternate mechanism such as host genetic adaptation may play a role in thermal tolerance of these colonies. Bleached corals recovered their symbionts within 1–3 mo (excepting 1 mortality) and remained C-dominated. However, colonies recovered 3 times faster at the northern reef, which experiences similar temperature but lower irradiance and higher water flow and turnover compared to the southern reef. This work indicates that both biotic (e.g. symbiont and host genotypic) and abiotic (e.g. hydrodynamic) factors influence the natural resistance and recovery of *M. capitata*, which can inform ecological predictions and conservation strategies for coral reefs under climate change.

KEY WORDS: Coral bleaching · Symbiosis · *Montipora capitata* · *Symbiodinium* · Kāneʻohe Bay

INTRODUCTION

Coral bleaching is occurring with increasing frequency and severity due to anthropogenic climate change and may soon occur annually on reefs worldwide (van Hooidonk et al. 2013), threatening the persistence of coral reef ecosystems. Bleaching in response to high temperatures involves the stress-induced loss of symbiotic algae (*Symbiodinium* spp.) that normally provide corals their color and primary source of energy; this loss of symbionts is reversible but can result in mortality when prolonged or severe (Hoegh-Guldberg 1999). To survive frequent and severe thermal stress, therefore, corals must either (1) resist bleaching, or (2) recover rapidly enough to tolerate the next thermal stress event.

Resistance to bleaching is highly variable both among and within coral species, owing to the genetic identity of the coral host, its symbionts, and their interaction (Edmunds 1994, Fitt & Warner 1995, Marshall & Baird 2000, Baird et al. 2009, Grottoli et al. 2014). Within a coral species, colonies hosting thermally tolerant symbionts (e.g. *Symbiodinium* clade D) may resist bleaching while colonies with thermally sensitive symbionts bleach severely (Glynn et al. 2001, Berkelmans & van Oppen 2006, Sampayo et al. 2008, Silverstein et al. 2015); changes in the dominant symbiont after bleaching (i.e. symbiont 'shuf-

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fling') may allow some corals to become more heat-tolerant (Baker 2001). However, the coral host may also mediate thermotolerance by a variety of mechanisms (Baird et al. 2009) that may arise through acclimatization using gene expression (Barshis et al. 2013), transgenerational epigenetic inheritance (Putnam & Gates 2015), and genetic adaptation (Dixon et al. 2015). Identifying resistant corals, and the particular host and symbiont traits underlying their resistance, is critical to understanding the present and future ecology of coral reefs.

Corals that are not resistant to bleaching may subsequently recover their symbionts, though the time to recovery can vary from a few weeks to as long as a year (Jokiel & Coles 1977, Szmant & Gassman 1990, Fitt et al. 1993, Jones & Yellowlees 1997, Toller et al. 2001). Moreover, due to the energetic debt incurred while bleached, corals may have reduced biomass, lipids, growth, and reproduction long after their symbionts return (Fitt et al. 1993, Rodrigues & Grottoli 2007, Levitan et al. 2014), and they may be more susceptible to repeated stress (Grottoli et al. 2014) and disease (Rogers et al. 2009). Since these negative impacts are likely to worsen the longer a coral remains bleached, symbiont recovery rates may determine the future success of a colony. Despite this importance, the rates at which symbionts repopulate bleached corals are not well understood. Both abiotic and biotic factors such as light, temperature (Cunning et al. 2015), flow (Nakamura et al. 2003), heterotrophy (Connolly et al. 2012), symbiont density-dependence (Jones & Yellowlees 1997), and environmental symbiont availability may influence recovery; however, the rates and variability of individual coral recovery have not been widely studied, especially in the field.

In late 2014, corals in Kāneʻohe Bay, Oʻahu, Hawaiʻi, USA, bleached for the first time since 1996 when temperatures reached 29–30°C (Bahr et al. 2015), surpassing the typical summertime maximum of 27–28°C (Jokiel & Brown 2004). Here, we study patterns of resistance and recovery of *Montipora capitata*, a dominant reef-building coral that forms symbioses with *Symbiodinium* in clade C and clade D (LaJeunesse & Thornhill 2011, Stat et al. 2013). Divergent responses were observed among *M. capitata* colonies, with some bleaching completely while others appeared unaffected. To understand variability in the resistance and subsequent recovery of these corals, we monitored the abundance of clade C and D *Symbiodinium* in bleached and non-bleached colonies for 6 mo after the bleaching event at 3 reef sites. Sites were chosen in the northern, central, and southern sectors of the bay to capture a gradient of decreasing oceanic influence (Smith et al. 1981) and investigate its impact on recovery dynamics. This environmental variability, and the multiple symbiont partners of *M. capitata*, create an ideal system in which to investigate factors influencing coral bleaching and recovery. In this study, we test whether (1) symbiont type is associated with bleaching in *M. capitata*, (2) symbiont shuffling occurs in *M. capitata*, and (3) recovery rates vary among reef locations.

MATERIALS AND METHODS

Study design and location

To analyze patterns of bleaching and recovery of *Montipora capitata* across Kāneʻohe Bay, Oʻahu, Hawaiʻi, USA, we repeatedly measured symbiont abundance in tagged colonies at 3 patch reefs located in the northern (Reef 44: 21° 28′ 36.4″ N, 157° 50′ 01.0″ W), central (Reef 25: 21° 27′ 40.3″ N, 157° 49′ 20.1″ W) and southern (HIMB [Hawaiʻi Institute of Marine Biology]: 21° 26′ 06.0″ N, 157° 47′ 27.9″ W) regions of Kāneʻohe Bay (Fig. 1), along a gradient of decreasing oceanic influence. At each reef, 10 pairs of adjacent bleached and non-bleached colonies (Fig. 1, inset) were tagged at 1–3 m depth along a 50–100 m transect following the reef edge (n = 60 colonies total). Colonies were first tagged and

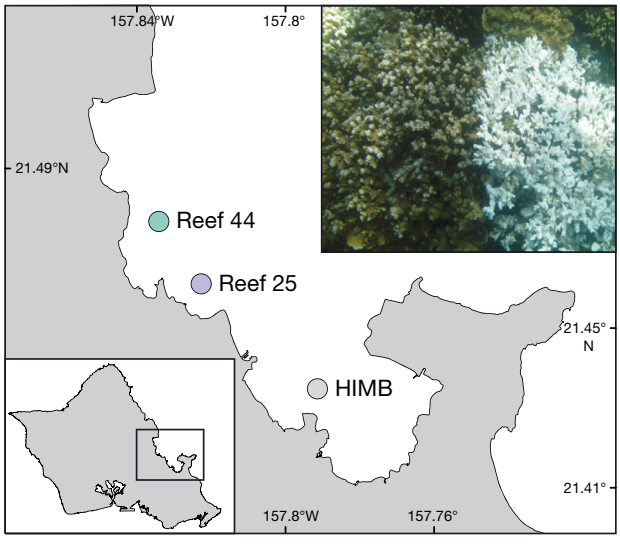

Fig. 1. Study reef locations in Kāneʻohe Bay, Oʻahu, Hawaiʻi, USA. HIMB: Hawaiʻi Institute of Marine Biology. Photograph inset shows example of one bleached (right) and non-bleached (left) pair of *Montipora capitata* colonies at the beginning of the study (photo credit: Raphael Ritson-Williams)

sampled on 24 October 2014, during the peak of a thermal stress and bleaching event, and they were categorized as 'bleached' or 'non-bleached' based on their appearance on this date (Fig. 1, inset). Throughout the study, colonies remained categorized as 'bleached' or 'non-bleached' reflecting their initial visual bleaching status, and no further visual assessments were made. Rather, recovery dynamics over the next ~6 mo were analyzed quantitatively by resampling each tagged colony on 4 November, 24 November, 16 December, 14 January, and 6 May 2015 (n = 6 time points). In sum, we sampled 10 (initially) bleached and 10 non-bleached colonies at each of the 3 reefs, at each of the 6 time points. While only one colony died during this period, several others were randomly missed during sampling or lost due to boat strikes, resulting in a total set of n = 334 samples.

Sample collection

Small branch fragments (~4–5 cm) were removed from the upper surface of each colony, frozen in liquid nitrogen, and transported to the Hawai'i Institute of Marine Biology, where they were stored at −80°C until processing. Small tissue biopsies (~1 cm^2) were subsampled from each fragment into 500 µl of DNA buffer (0.4 M NaCl, 0.05 M EDTA) with 1% (w/v) sodium dodecyl sulfate (SDS). On 4 November and 16 December 2014, small tissue biopsies were removed directly from colonies into DNA buffer. DNA was extracted from each sample using a modified CTAB-chloroform protocol (dx.doi.org/10.17504/protocols.io.dyq7vv).

Symbiont community analysis

Quantitative PCR was used to determine the symbiont to host (S/H) cell ratio (Mieog et al. 2009b) of clade C and D *Symbiodinium* in each sample. Assays quantifying specific actin loci in clade C and D *Symbiodinium* were performed following the methods of Cunning & Baker (2013). Based on both internal transcribed spacer (ITS2) and actin gene sequencing from a subset of samples, we expect only specific clade C- and D-types, for which target specificity of clade level primers was confirmed (see the Supplement at www.int-res.com/articles/suppl/m551p131_supp.pdf). To quantify coral host DNA, an assay was developed targeting the single-copy PaxC intron of *Montipora capitata* (see Table S1 in the Supplement). All samples were run for each assay in duplicate 10 µl reactions on a StepOnePlus platform (Applied Biosystems) for 40 cycles, with a relative fluorescence (ΔR_n) threshold of 0.01 and baseline interval of cycles 3–20. After data quality filtering, symbiont to host cell ratios for clade C and D symbionts in each sample were calculated by the formula $2\text{^}(C_T^{host} - C_T^{symbiont})$, where C_T is cycle threshold, and normalized for differences in probe fluorescence intensity and target locus gene copy number (see the Supplement). Total S/H ratios were calculated as the sum of clade C and D S/H ratios.

Data analysis

Differences in proportions of clade C and D dominance between bleached and non-bleached colonies and among reefs were assessed by chi-squared tests. Generalized linear models were used to analyze binomial responses of symbiont shuffling and presence of background symbionts in relation to bleaching, reef, dominant symbiont, and time (with a random effect of colony included when appropriate), with likelihood ratio tests (LRTs) identifying significant predictors. Log-transformed total S/H ratios at each sampling were analyzed by linear models with reef, bleaching, and dominant symbiont clade as crossed categorical predictors, for which significance was assessed by partial *F*-tests. Trajectories of symbiont abundance over time were modeled by a linear mixed model (package lme4, Bates et al. 2015) with fixed effects of reef, bleaching, dominant symbiont clade, and time, random intercepts for each colony, and a general spline basis (package spida, http://spida.r-forge.r-project.org) allowing a quadratic effect of time before January, and a linear effect thereafter. Non-significant fixed effects were eliminated by backwards selection using *F*-tests with Satterthwaite's degrees of freedom approximation (package lmerTest, Kuznetsova et al. 2015), and 4 points with standardized residuals >2.5 were omitted from the model. Confidence intervals on fitted values were generated by parametric bootstrapping (n = 999) with random effects set to zero (package lme4). Hypothesis tests related to fitted models were conducted using linear contrasts implemented in package lsmeans (Lenth 2015) with alpha = 0.05 and p-values adjusted to control family-wise error rates. All analyses were performed using R v3.2.2 (R Core Team 2015). All data and scripts to reproduce the analyses and figures in this paper are archived at Zenodo (Cunning 2016).

RESULTS

Symbiodinium community structure

Quantitative PCR assays detected clade C and D *Symbiodinium* either alone or in mixtures (Fig. 2). Across samples from all time points (n = 334), 55% contained C only, 10% contained D only, and 35% contained both C and D. The clade composition of mixed samples ranged from 99.97% clade C to 99.99% clade D with many values near these extremes, although over half of mixed samples contained >10% of the non-dominant symbiont clade (Fig. 2 inset). The percentage of colonies (n = 60, sampled 3–6 times each) in which both C and D were detected at least once was 60%, with the remainder having C only (37%) or D only (3%) in all samples. The overall dominant symbiont (with the highest mean relative abundance in all samples of the colony) was clade C in 73% of colonies, and clade D in the remaining 27% (note this was not a random sample of the population due to the targeting of bleached and non-bleached pairs). Sequencing of *Symbiodinium* ITS2 from a subset of samples revealed ITS2 types C31 and D1a as the particular members of clades C and D in these colonies (see the Supplement).

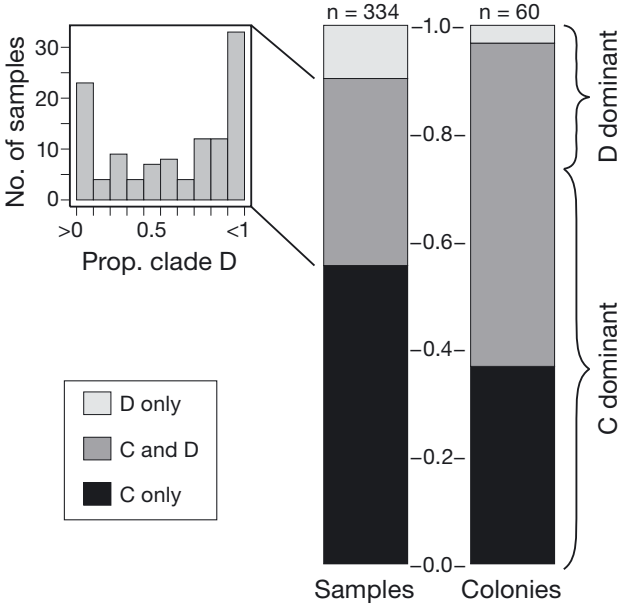

Fig. 2. Occurrence of *Symbiodinium* clades C and D in *Montipora capitata* samples and colonies (each colony comprises 3–6 samples due to repeated sampling). The relative abundance of clades C and D in mixed assemblages is shown in the histogram inset (upper left). Brackets indicate the proportion of colonies dominated by clade C or clade D *Symbiodinium*

Influence of *Symbiodinium* on bleaching response

There was a significant relationship between a colony's dominant *Symbiodinium* clade and whether it visually bleached ($p < 0.0001$); 100% of bleached corals (n = 30) were dominated by clade C, and 100% of D-dominated corals (n = 16) did not bleach (Fig. 3A). However, some C-dominated corals (n = 14) also did not bleach. Symbiont abundance in October did not differ between non-bleached C-dominated colonies and those dominated by clade D ($p = 0.52$) but was reduced in bleached corals by 88% (0.011 vs. 0.091 S/H; $p < 0.0001$; Fig. 3B). Within C-dominated corals, there was no difference in the presence of background clade D *Symbiodinium* between colonies that bleached and those that did not bleach ($p = 0.16$; Fig. 4). There was also no effect of reef location on October symbiont abundance in bleached corals ($p = 0.77$) or on the prevalence of C or D dominance in non-bleached corals ($p = 0.12$).

Temporal patterns in *Symbiodinium* composition

The dominant symbiont clade remained the same over time in 80% of colonies, while 20% showed variability in the dominant symbiont clade (Fig. 4). However, this variability was not related to bleaching ($p = 0.19$), reef location ($p = 0.11$), or dominant symbiont clade ($p = 0.11$). The changes that occurred were mostly transient, in either direction (i.e. C to D and D to C) and were not related to date ($p = 0.06$) or bleaching ($p = 0.62$). The presence of background symbiont clades also fluctuated but with no relationship to date or bleaching ($p > 0.10$ for all LRTs).

Temporal patterns in *Symbiodinium* abundance

At the beginning of the study, *Symbiodinium* abundance in bleached *Montipora capitata* was 0.011 (geometric mean symbiont to host cell ratio [S/H]) and did not vary among reefs ($p = 0.77$). By the 14 January sampling, symbiont abundance had increased to 0.234 S/H, and again did not vary among reefs ($p = 0.89$), or between previously bleached and non-bleached corals ($p = 0.16$). However, the trajectories of symbiont populations over this time period differed significantly depending on bleaching and reef ($p = 0.002$; Table 1, Fig. 5). At Reef 44, symbiont abundance in bleached corals increased rapidly and was not significantly different than non-bleached corals ($p > 0.05$) after 26 d (19 November 2014). At

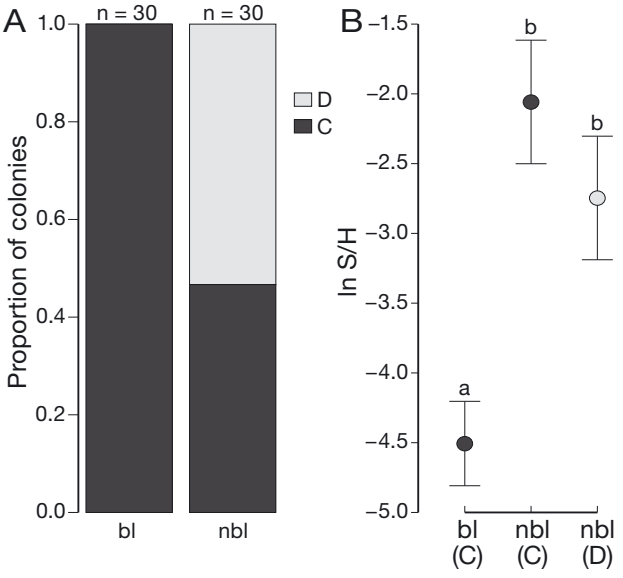

Fig. 3. Influence of *Symbiodinium* on bleaching in *Montipora capitata*. (A) Proportions of bleached (nl) and non-bleached (nbl) colonies that were dominated by clade C or clade D *Symbiodinium*. (B) Total symbiont abundance (symbiont to host cell ratio, S/H) in October (peak of bleaching event) in bleached colonies dominated by clade C, non-bleached colonies dominated by clade C, and non-bleached colonies dominated by clade D. Groups not sharing letters are significantly different (Tukey's, adjusted $p < 0.05$)

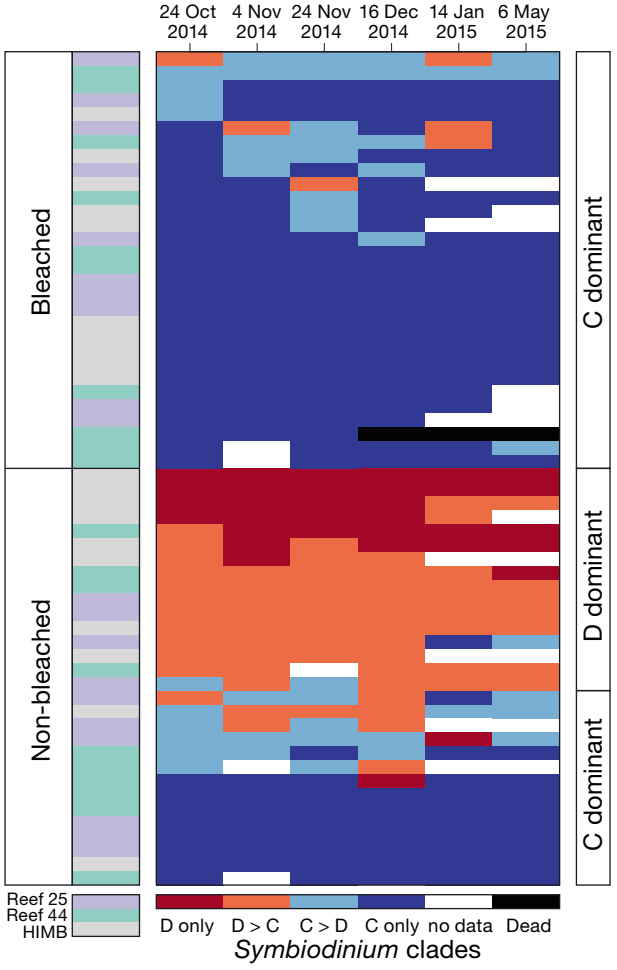

Fig. 4. *Symbiodinium* clade composition in individual colonies over time. Heatmap rows represent coral colonies, sorted by bleaching and dominant symbiont clade, with columns for each sampling time point. Heatmap colors indicate the relative abundance of *Symbiodinium* clade C and/or D in each sample. White rectangles indicate samples randomly missed during sampling or lost due to boat strikes, while 1 coral colony died (black rectangles) before the 16 December sampling. Row side colors indicate the source reef of each colony

Reef 25, symbionts in bleached corals recovered to the same level as non-bleached corals after 61 d (24 December 2014), while at HIMB, equivalent recovery took 81 d (13 January 2015).

Relative to January, when symbiont abundance in all corals was highest (0.234 S/H), non-bleached corals contained ~60% fewer symbionts in October (0.091 S/H) and May (0.093 S/H). At this final time point, mean abundance was lower at HIMB than Reef 44 ($p = 0.03$), and in previously bleached than non-bleached corals ($p = 0.004$).

Table 1. Fixed-effects ANOVA for linear mixed model describing trajectories of symbiont abundance (shown in Fig. 5). Pseudo-$R^2 = 0.67$ (squared correlation between fitted and observed values). Numerator and denominator degrees of freedom (Num df and Den df) are calculated using Satterthwaite's approximation

	SS	MS	Num df	Den df	*F*	p(>*F*)
Time	109.008	36.336	3	237.88	27.418	0
Bleach	69.827	69.827	1	168.245	52.69	0
Reef	1.333	0.666	2	168.142	0.503	0.606
Time:Bleach	19.246	6.415	3	237.88	4.841	0.003
Time:Reef	26.21	4.368	6	237.689	3.296	0.004
Bleach:Reef	4.324	2.162	2	168.142	1.631	0.199
Time:Bleach:Reef	28.314	4.719	6	237.689	3.561	0.002

DISCUSSION

Colonies of *Montipora capitata* in Kāneʻohe Bay, Oʻahu, Hawaiʻi, USA, were dominated by either clade C or clade D *Symbiodinium*. While individual samples contained both clades 35% of the time, repeated sampling of colonies revealed that 60% contained both clades at one or more time points. Colonies displayed divergent responses to elevated seawater temperatures in October 2014, with some turn-

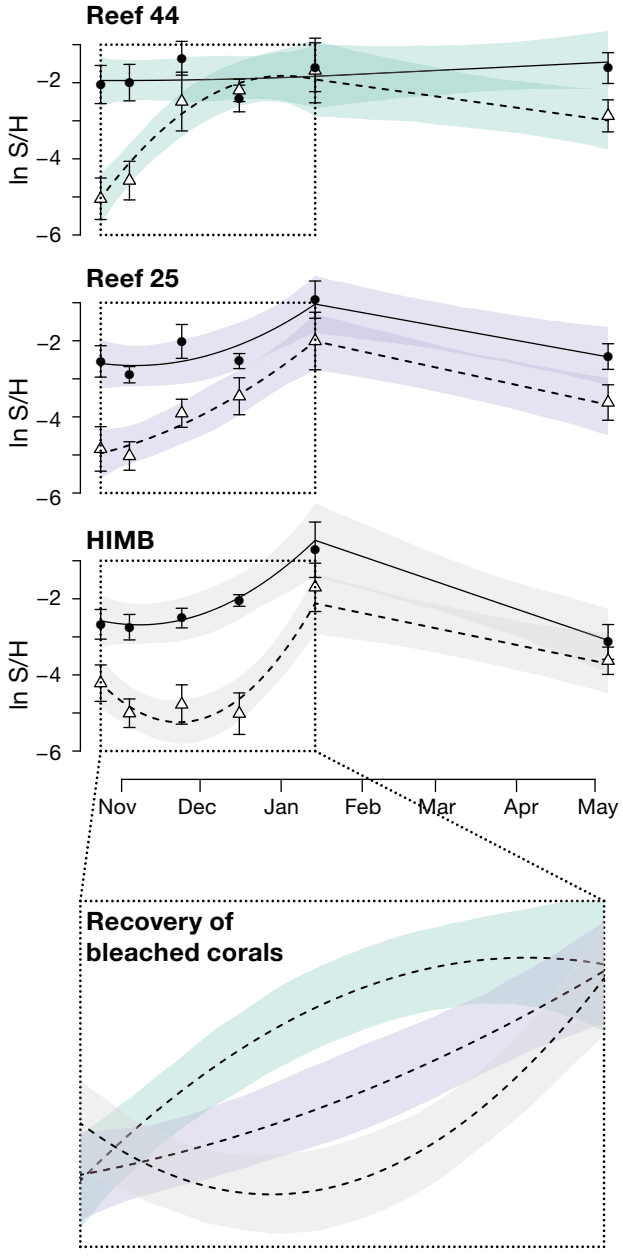

Fig. 5. *Symbiodinium* population trajectories in bleached and non-bleached corals at each reef. Points represent mean total log symbiont to host cell ratio (S/H) ratios (solid circles = non-bleached; open triangles = bleached) with error bars ±1 SE. Lines represent fitted model values (solid = non-bleached; dashed = bleached) with shaded 90% confidence bands (unique colors for each reef match Figs. 1 & 4). Zoomed inset superimposes fitted values and confidence bands for bleached corals at each reef between 24 October and 14 January for comparison among reefs

ing completely white while neighboring colonies remained darkly pigmented (Fig. 1). This variability was strongly, but not completely, related to the colony's dominant symbiont clade: all bleached colonies were dominated by C, while all colonies dominated by D did not bleach; however, some colonies dominated by C also did not bleach. Although pre-bleaching samples were not obtained, corals likely had the same dominant symbiont; the possibility that bleached corals with clade C were dominated by D prior to bleaching (or that non-bleached corals rapidly changed symbionts without bleaching) is inconsistent with observations that symbiont changes (when they occur) typically involve a shift to D dominance after bleaching (Silverstein et al. 2015). Thus, while a link between symbiont identity and thermal tolerance had not been directly investigated in *M. capitata* (but see Stat et al. 2013), it is shown here to be consistent with other corals such as *Acropora millepora* on the Great Barrier Reef (Berkelmans & van Oppen 2006, Mieog et al. 2009a), *Pocillopora damicornis* in the eastern Pacific (Glynn et al. 2001), and *Montastraea cavernosa* in the Caribbean (Silverstein et al. 2015), which are more heat tolerant when partnered with clade D compared to clade C symbionts (but see Abrego et al. 2008). However, in striking contrast to these other species, in which all colonies with thermally sensitive clade C symbionts bleached, some colonies of *M. capitata* that were clade C-dominated did not bleach, indicating that for some corals factors other than symbiont clade also control thermal tolerance.

In fact, nearly half of the non-bleached *M. capitata* colonies were dominated by clade C symbionts, with densities as high as those in clade D-dominated colonies (Fig. 2). One possible explanation for why some C colonies resisted bleaching while others did not is that they contained different clade C types; however, sequencing of *Symbiodinium* ITS2 from a subset of samples revealed the same dominant type (C31) in both bleached and non-bleached colonies (see Fig. S1 in the Supplement), so bleaching resistance cannot be attributed to different clade C symbionts. Previous work on *M. capitata* also demonstrates high specificity within clade C for C31 (LaJeunesse & Thornhill 2011, Stat et al. 2013). While genetic markers with higher resolution than ITS2 (Finney et al. 2010, LaJeunesse & Thornhill 2011) might differentiate *Symbiodinium* C31 in resistant and susceptible colonies, it is also possible that these observed differences in thermal tolerance are driven by the coral host.

The coral host itself may mediate thermal tolerance by a variety of mechanisms implicated in photoprotection, antioxidant systems, and stress responses (Baird et al. 2009). Resistant and sensitive corals may be differentiated by either possession or expression of these traits, and thus thermal tolerance may arise from either adaptation or acclimatization. Exposure to

certain environmental conditions (such as high variability or previous stress) may induce beneficial acclimatization (Huey et al. 1999) that can increase performance and stress-tolerance (Barshis et al. 2013, Brown et al. 2015). However, this phenomenon is unlikely to explain the difference between resistant and sensitive colonies here since they occur immediately adjacently on the reef and have experienced the same environment. Divergent phenotypes in individuals with the same symbionts and environmental history may be more likely attributable to host adaptation. Consequently, these non-bleached, C-dominated colonies of *M. capitata* may be excellent candidates for investigating the biology of thermal tolerance and for selective breeding applications to build coral reef resilience (van Oppen et al. 2015). Our results suggest that *M. capitata* may resist bleaching by multiple mechanisms — either by associating with thermally tolerant symbionts or through host-mediated adaptation.

Corals that do not resist bleaching may subsequently acquire thermal tolerance by acclimatization through 'shuffling' the relative abundances of different symbiont types (Baker 2001). Sixty-five percent of *M. capitata* colonies hosted both clades C and D simultaneously, and the detection of mixtures increased with sampling effort (Fig. 2), suggesting there is potential for symbiont shuffling in this species. However, 80% of colonies showed no variation in the dominant symbiont throughout the study, while 20% showed transient changes that did not correlate with bleaching, reef location, or time (Fig. 4). These seemingly random changes in clade dominance in a minority of colonies may be explained by intracolony spatial variation in symbiont assemblages (Rowan et al. 1997), though we tried to minimize this impact by sampling only upper colony surfaces. In any case, the simultaneous high prevalence of mixed communities but low occurrence of symbiont shuffling is consistent with *P. damicornis* in the eastern Pacific (McGinley et al. 2012) and indicates that either (1) the dominant symbiont is immutable in adult colonies of these species, or (2) the particular conditions of disturbance and recovery did not favor symbiont shuffling in this case (McGinley et al. 2012, Cunning et al. 2015). Evaluation of these hypotheses, and the relevance of symbiont shuffling for *M. capitata*, will require further experimental investigation of intracolony spatial and temporal variation in symbiont communities.

A remarkable result of this study is that only one colony suffered mortality from bleaching, while the rest fully recovered their symbiont populations in less than 3 mo (Fig. 5). This extent and duration of recovery is consistent with visual observations of previous bleaching events in Kāneʻohe Bay (Jokiel & Brown 2004), suggesting these corals are highly resilient. However, symbiont repopulation does not necessarily indicate full recovery from stress; other physiological parameters such as biomass, protein and lipid content, and reliance on heterotrophy may remain impacted for several months to more than a year (Rodrigues & Grottoli 2007, Baumann et al. 2014). While heterotrophy can help compensate for reduced symbiont autotrophy in bleached *M. capitata* (Grottoli et al. 2006), recovery of symbionts is nevertheless prerequisite to the replenishment of lost energy reserves and return to a healthy state. Consequently, the rate of symbiont repopulation may be predictive of overall recovery, and variation in repopulation rates may lead to differences in future performance, including growth, reproduction, and stress tolerance. Given these expectations, our finding that symbiont recovery took over 2 and 3 times as long at Reef 25 and HIMB relative to Reef 44 (Fig. 5) indicates potentially significant disadvantages in the health status and future performance of these corals, especially in the face of repeated stress events.

The variation in recovery rates across Kāneʻohe Bay may be driven by a variety of abiotic or biotic factors. Temperature is an obvious candidate; however, daily mean temperature (Ritson-Williams & Gates 2016a) during recovery did not differ among reefs (Fig. S2A in the Supplement). Light data (Ritson-Williams & Gates 2016b) were not obtained during early recovery or from Reef 25, but available measurements were 21% higher at HIMB than Reef 44 (Fig. S2B). Because light is amplified in bleached corals due to reduced symbiont self-shading (Marcelino et al. 2013), higher external irradiance may exacerbate or prolong stress to *Symbiodinium* in bleached and recovering corals. Thus, while it is difficult to draw conclusions from single light sensors in highly heterogeneous reef light environments (Wangpraseurt et al. 2014), higher irradiance at HIMB could have slowed coral recovery from bleaching.

Another factor that differs dramatically among reef locations is the hydrodynamic regime: estimated water velocity and turnover are high at Reef 44, intermediate at Reef 25, and low at HIMB, leading to over 30-fold variation in residence times (Lowe et al. 2009). Indeed, the primary feature differentiating the 3 sectors of the bay is the decreasing degree of oceanic influence from north to south, resulting in reduced water flow and exchange with the open ocean around HIMB (Smith et al. 1981, Lowe et al. 2009).

Higher water flow at Reef 44 may benefit bleached corals by increasing nutrient delivery and waste removal across boundary layers, while also increasing heterotrophic food delivery (Fabricius et al. 1995), which may energetically subsidize recovery of the symbiont population (Hughes et al. 2010). Indeed, experimental work has shown that water flow accelerates recovery from bleaching (Nakamura et al. 2003). This study provides field data consistent with this finding and suggests that corals in high flow areas may recover more rapidly from bleaching and be better able to tolerate repeated thermal stress events.

While water flow and oceanic influence are greater in the northern bay, this region also receives more terrestrial runoff (Smith et al. 1981). Together, these factors may impact dynamics of nutrients, pollutants, freshwater, sediments, and benthic and planktonic communities (Smith et al. 1981), which may in turn impact coral recovery from bleaching in complex ways. Other possible mediators of bleaching recovery rates are microbial communities (Bourne et al. 2008), and even the *Symbiodinium* metacommunity. If corals acquire symbionts from the surrounding environment during recovery from bleaching, then the diversity and abundance of symbionts in the water column, sediments, and nearby coral hosts may influence the recovery process. While there is no information about the spatial and temporal variation in *Symbiodinium* in the environment surrounding these reefs, this would be a valuable topic of future investigation.

In summary, we show that hosting clade D *Symbiodinium* provides resistance to thermal stress in *M. capitata* but that some colonies with clade C are also stress-resistant. Following stress, we found that recovery of bleached corals was much faster at the reef with the highest water flow and turnover time. Together, these results elucidate biotic and abiotic factors that influence bleaching resistance and resilience. This work can help both scientists and managers target future investigations and conservation strategies, which may include assisted evolution or transplantation.

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