

Coral thermal stress and bleaching enrich and restructure reef microbial communities via altered organic matter exudation

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ABSTRACT

Coral bleaching is a well-documented and increasingly widespread phenomenon in reefs across the globe, yet there has been relatively little research on the implications for reef water column microbiology and biogeochemistry. A mesocosm heating experiment and bottle incubation compared how unbleached and bleached corals alter dissolved organic matter (DOM) exudation in response to thermal stress and subsequent effects on microbial growth and community structure in the water column. Thermal stress of healthy corals tripled DOM flux relative to ambient corals and DOM exudates from stressed corals (heated and/or previously bleached) were compositionally distinct from healthy corals. These exudates significantly increased bacterioplankton densities up to twice that of (3E6 cells/mL) of bacterioplankton grown on healthy coral exudates and engendered a consistent, significant shift in bacterioplankton communities towards increased proportions of copiotrophic Alteromonadaceae, Flavobacteriaceae, and Saprospiraceae families as well as putative

35 pathogens in the Pseudoalteromonadaceae and Colwelliaceae families. Together these results
36 demonstrate how the impacts of both short-term thermal stress and long-term bleaching may
37 extend into the water column, with altered coral DOM exudation driving microbial feedbacks that
38 influence how coral reefs respond to and recover from mass bleaching events.

INTRODUCTION

Coral reef ecosystems are engineered by benthic primary producers via interactions with the water column, and unraveling these interactions is a critical step in understanding how healthy reefs function and how to prevent their degradation. Corals and algae influence the surrounding water column biogeochemistry (Atkinson, 1987; Lewis, 1977; Moberg & Folke, 1999; Odum & Odum, 1955; Smith et al., 2013) by providing fixed carbon substrates to primary consumers through dissolved organic matter (DOM) exudation (Crossland, 1987; Ferrier-Pages et al., 1998; Ferrier-Pagès et al., 2000; van Duyl & Gast, 2001). Reef benthic primary producers can release upwards of 30% of their daily photosynthate into the water column in the form of DOM, which can serve as a carbon and nutrient source for bacterioplankton (Ducklow, 1990; Haas et al., 2011). Coral DOM exudates have unique fluorescent DOM signatures (fDOM), dissolved combined neutral sugars (DCNS) compositions, and organic compound mass spectrometry profiles compared to DOM exudates from the surrounding seawater and other benthic primary producers (Nelson et al., 2013; Quinlan et al., 2018; Wegley Kelly et al., 2022). Beyond DOM serving as an energy and nutrient source for bacterioplankton, the unique quality of different DOM exudates may elicit distinct physiological changes in bacterioplankton communities as they respond to the chemical cues exuded by different benthic primary producers.

Coral DOM exudation facilitates the interaction between the coral holobiont and the surrounding bacterioplankton. Coral reef bacterioplankton exhibit chemotactic responses to a variety of DOM released by corals, including dimethylsulfoniopropionate (DMSP) (Tout et al., 2015). DOM exudates from coral also support the growth and activity of distinct heterotrophic bacterioplankton communities (Haas et al., 2011, 2013; Nakajima et al., 2018; Nelson et al., 2013; Silveira et al., 2017). *In situ* studies have identified unique metabolites and microbial communities adjacent to corals compared to the surrounding seawater (Silveira et al., 2017; Tout et al., 2014; Walsh et al., 2017; Weber et al., 2019). These microbial communities are

enriched in genes related to chemotaxis, motility, and signal transduction, suggesting that these regions surrounding corals contain bacterioplankton with the metabolic capacity to directly interact with corals (Ochsenkühn et al., 2018; Silveira et al., 2017; Tout et al., 2014; Walsh et al., 2017). This zone of interaction is an essential area for feedback loops between the benthos and the water column in the coral reef ecosystem, as changes in bacterioplankton may influence coral physiology. Despite the burgeoning knowledge of how healthy corals influence bacterioplankton via DOM exudation, relatively little is known about if and how this relationship changes when corals are stressed.

One major stressor corals experience is ocean warming, with marine heatwaves occurring more frequently due to global climate change (Arias et al., 2021; Cooley et al., 2022; Levitus et al., 2012). Thermal stress harms corals via bleaching, a well-documented and widespread phenomenon in which the symbiosis between corals and Symbiodinaceae breaks down as corals are exposed to elevated temperatures for an extended period of time (Brown, 1997). Mass coral bleaching has been recorded since 1979 and has increased in frequency, with a 3-fold increase in bleaching events in 2006-2012 compared to 1985-1991, restricting the time for coral reefs to recover between bleaching events (Cooley et al., 2022; Heron et al., 2016; van Hooidonk et al., 2016). Although corals can recover from bleaching, they will die if thermal stress persists (Hoegh-Guldberg, 1999). Even at sub-lethal levels, coral bleaching alters the coral holobiont's metabolism (Innis et al., 2021), its chemistry (Roach et al., 2021), and microbiota (Bourne et al., 2016; Liang et al., 2022; Littman et al., 2011; McDevitt-Irwin et al., 2017; Oppen & Blackall, 2019; Thurber et al., 2009).

Recent research suggests that coral-water column interactions are altered during periods of elevated temperatures (Garren et al., 2014; Niggli et al., 2009; Tremblay et al., 2012). Niggli *et al.* (2009) found that bleaching corals released elevated levels of particulate nitrogen (PN) and particulate organic carbon (POC) into the water column. In another study, heated *Stylophora pistillata* corals showed a change in total organic carbon (TOC) flux direction,

91 transitioning from negative flux in healthy corals (uptake) to positive flux in heated/bleached
92 corals (release) (Tremblay et al., 2012). These alterations to water column chemistry likely shift
93 the bacterioplankton community composition as specific taxa respond to metabolites released
94 by stressed corals. In one study, the bacterial pathogen *Vibrio coralliilyticus* responded to DMSP
95 as a chemotactic cue when it was released at elevated concentrations by heat stressed coral
96 (Garren et al., 2014). Even under ambient conditions, coral mucus elicits a rapid chemokinetic
97 and transcriptional response in *Vibrio coralliilyticus*, further suggesting that this pathogen uses
98 coral chemical cues to trace and target its host (Gao et al., 2021). Given that healthy corals
99 exude DOM into the surrounding seawater and influence subsequent bacterioplankton
100 dynamics, we hypothesized that 1) thermal stress and bleaching can dramatically alter DOC
101 exudation rates and DOM composition with cascading effects on bacterioplankton growth and
102 community structure and 2) short-term thermal stress and long-term bleaching will have different
103 effects. These different effects will help elucidate how the succession of bleaching, from onset
104 to recovery or death, influences the succession of DOM and bacterioplankton *in situ*.

RESULTS

Experimental Design

We tested these hypotheses during a mass bleaching event on Mo'orea, French Polynesia. In April 2019, the reefs of Mo'orea bleached after a prolonged period of high water temperatures (Leinbach et al., 2021; Speare et al., 2021) (Figure 1). In May 2019, immediately following this thermal stress event, we leveraged the natural distributions of recently bleached and unbleached corals to elucidate the independent and combined impacts of experimentally-induced thermal stress and recent bleaching on coral DOM exudation and subsequent bacterioplankton remineralization and growth. In brief, coral nubbins from three different species (*Pocillopora verrucosa*, *Acropora pulchra*, and *Porites rus*) assigned to both bleached and unbleached phenotypes were collected and exposed to seven days of either ambient (28.6 °C) or elevated water temperatures (32 °C +/- 0.2 °C) and ambient light levels in flow through aquaria (n=3 per treatment) (Fig 1A.I). The combination of bleaching level and temperature yielded four treatments representing a factorial cross of prior bleaching phenotype and temperature: "Control", "Heated", "Bleached", and "Bleached + Heated" (Fig 1 A.II). Additionally, two water-only control aquaria, one for each temperature treatment, were included ("Negative Control" and "Negative Control + Heated"). After seven days of pretreatment, DOM exudates from each of the aquaria were collected (Fig 1.A.III) and used as growth media for dark incubation dilution cultures (Fig 1 A.IV). Unfiltered back-reef seawater was used as an inoculum representative of ambient back-reef bacterioplankton communities (Nelson et al., 2013). Dilution cultures were conducted in 1 L 10% acid-washed, triple milliQ rinsed (hereafter termed "acid washed") polycarbonate bottles in the dark at ambient temperatures for 36 hours and sampled at the beginning (n=3 per treatment) and end (n=3 per treatment) of the incubation. We used a combination of bulk DOC measurements, flow cytometry, 16S amplicon sequencing, and untargeted metabolomics to assess differences in the composition of DOM exudates and how these exudates altered microbial growth and community structure (Fig 1 A.V).

Symbiodiniaceae Densities

Symbiodiniaceae cell densities were used to assess individual and aquaria-wide bleaching levels of corals collected in the field and after the seven day pre-treatment, respectively. At collection, bleached corals had significantly lower Symbiodiniaceae cell densities (two-way ANOVA, $F=45.552$, $p=2.67e-08$). Coral species also had a significant effect on Symbiodiniaceae densities (two-way ANOVA, $F=4.738$, $p=0.0137$), as well as the interaction between coral species and bleaching (two-way ANOVA, $F=4.287$, $p=0.0199$) (Figure 1C).

After seven days of incubation at ambient and elevated temperatures, the average Symbiodiniaceae densities showed that the four coral treatments had varying degrees of bleaching (Figure 1D). Bleached corals had significantly lower Symbiodiniaceae densities (two-way ANOVA, $F=6.584$, $p=0.0333$). Heating did not have a significant effect on Symbiodiniaceae cell densities ($F=0.001$, $p=0.9727$), and neither did the interaction between heating and bleaching (two-way ANOVA, $F=1.284$, $p=0.2901$). Therefore the Control treatment had the highest Symbiodiniaceae densities during the exudation experiment. Heated aquaria exhibited slightly lower Symbiodiniaceae cell densities consistent with some paling, yet still had higher cell densities than their Bleached and Bleached + Heated counterparts.

Dissolved Organic Carbon

Control corals exuded roughly $5 \mu\text{M C}\cdot(\text{dm}^2)^{-1}\cdot\text{h}^{-1}$ while Heated corals and Bleached corals exhibited roughly 289% (mean $13.22 \mu\text{M C}\cdot(\text{dm}^2)^{-1}\cdot\text{h}^{-1}$) and 177% (mean $8.10 \mu\text{M C}\cdot(\text{dm}^2)^{-1}\cdot\text{h}^{-1}$) higher DOC fluxes. Bleached + Heated corals exhibited undetectable DOC flux. Although DOC exudation appeared to be affected by treatment, we were unable to elucidate significant differences in areal DOC flux rates possibly due to small sample size and short exudation times (Kruskal-Wallis chi-squared= 4.1667 , $p=0.244$) (Figure 2A). Coral treatments

generally had higher raw DOC concentrations than the water controls, although this effect was not significant (Kruskal-Wallis chi-squared=9.3187, $p=.09$) (Figure S2).

Microbial Growth

Flow cytometry revealed distinct microbial growth patterns between the DOM treatments. Two-way ANOVAs were used to test the effect of both timepoint and treatment on bacterioplankton cell concentrations. We found that bacterioplankton concentrations significantly increased through time in the dark bottle incubations (two-way ANOVA, $F=104.372$, $p<2.2E-16$) and differed significantly between treatments (two-way ANOVA, $F=53.685$, $p<2.2E-16$) (Figure 2B). All coral treatments had significantly higher cell concentrations than both the Negative Control and the Negative Control + Heated (Tukey post-hoc test, $p<0.05$). Within the coral DOM treatments, Heated exudates yielded significantly higher bacterioplankton concentrations than the Control (Tukey post-hoc test, $p<0.05$), with bacterioplankton grown on Heated DOM reaching concentrations of 3,160,000 cells/mL ($\pm 790,000$), nearly double that of the Control (1,562,000 cells/mL $\pm 137,000$) (Figure 2B). Bacterioplankton specific growth rate also differed significantly between the treatments (one-way ANOVA, $F=6.363$, $p=0.005$) (Figure S3).

Microbial Community Structure

The DOM derived from the six treatments yielded distinct microbial communities after 36 hours of growth. There was a significant change in microbial communities from the start to the end of the bottle incubations, indicating that communities changed through the bottle incubation and were not simply reflective of the starting communities (PERMANOVA, $F=72.033$, $R^2=0.71$, $p\leq.001$, Figure S4). After 36h, bacterioplankton grown on coral exudates were significantly different from those grown on water negative controls (PERMANOVA $F=8.679$, $R^2=0.40$, $p\leq.001$) (Figure 3A). Within the coral treatments, Controls maintained distinct community structure from the Heated, Bleached, and Bleached + Heated communities, hereafter

collectively referred to as “stressed” (PERMANOVA $F=2.822$, $R^2=0.59$, $p=0.009$). There was overlap within the stressed communities and a consistent shift in ordination space away from the Controls, indicating a potentially conserved change that occurs in microbial communities in response to stressed coral exudates.

Many eutrophic coastal-associated bacterial families were overrepresented in the negative controls including Nitrincolaceae and Methylophagaceae (Francis et al., 2021), as well as the common coral reef associated family Rhodobacteraceae (Apprill et al., 2021; Comstock et al., 2022; Haas et al., 2016; Kelly et al., 2019; Nelson et al., 2011). Coral DOM microbial communities were dominated by the families Alteromonadaceae and Rhodobacteraceae, although there was substantial variation between the four treatments (Figure 3B, Table S1). Control corals maintained distinct microbial communities from both negative controls and stressed corals, overrepresented in the families Cryomorphaceae, Litoricolaceae, and Halieaceae. Alteramonadaceae, a common marine copiotrophic family (Baumann et al., 1972), was lowest in communities grown on Control exudates (28.3%) and substantially higher in the communities growing on the stressed coral exudates (46.6%-38.6%). Pseudoalteromonadaceae also increased in abundance from Control communities to stressed communities (3.3% in Control, and a mean of 9.1% in stressed). The common coral reef-associated family Rhodobacteraceae was higher in the Control (21.3%) and lower in the three stressed treatments (13.7%-19.4%). Another common coral reef associated family, Cryomorphaceae, was abundant in the Control treatment (13.0%) and then reduced in abundance in the stressed treatments (5.6%-7.2%). Microbial community alpha diversity metrics (observed sequences, Chao diversity, Shannon diversity, and Shannon’s Evenness) were assessed after 36 hours of growth (Figure S5), with none of these indices being significantly affected by treatment (one-way ANOVA, $p \geq .05$).

Bacterial Taxa Differential Abundance Analysis

Multivariate analysis demonstrated that stressed corals enriched distinct bacterioplankton communities compared to their Control counterparts. In order to directly elucidate which specific bacterial taxa were driving these differences, we performed DESeq2, (see supplementary methods) on a subset of the data that only included the four coral DOM treatments (Love et al., 2014), yielding a final count of 159 OTUs to be run through DESeq2. The log₂ fold-change of OTU abundances was calculated between the three coral stress treatments and the coral controls to elucidate OTUs that were differentially abundant when corals were bleached and/or heated (Table S2) (Figures 3C and S6).

A total of 31 significantly differentially abundant bacterial OTUs (19.5%) were identified by DESeq2 (DESeq2, log₂ fold-change>0, p≤.05 after FDR adjustment, Table 1, Figures 3C, S6, and S7). These OTUs belonged to four bacterial and one archaeal class: Alphaproteobacteria, Gammaproteobacteria, Bacteroidia, Deltaproteobacteria, and Thermoplasmata, with the majority (64.5%) of differentially abundant OTUs belonging to Gammaproteobacteria. Within Gammaproteobacteria, there was a significant enrichment of numerous abundant Alteromonadaceae and Pseudoalteromonadaceae OTUs in at least one of the three treatments (75% of all differentially abundant Gammaproteobacteria OTUs).

In all three stress treatments there was a significant enrichment of two *Pseudoalteromonas* OTUs (1224 and 1296), one *Alteromonas* OTU (734), and one unclassified Saprospiraceae OTU (322). All three stress treatments also showed an enrichment of a highly abundant *Alteromonas* OTU (2), although this was only statistically significant in the Bleached and Heated treatments. There were 12 differentially abundant OTUs found only to be significant in the Bleached treatment including significant enrichment in members of the genus *Pseudoalteromonas* (OTUs 75 and 85), unclassified Saprospiraceae (OTU 101), and *Phaeocystidibacter* (OTU 480), and significant reductions in members of the genus *Litoricola* (OTUs 27 and 419) and unclassified Alteromonadaceae (OTUs 368, 1012, and 1023). The two heated treatments had significant enrichment in OTUs of the genus *Pseudoalteromonas* (OTU

853), *Aestuariibacter* (OTU 48), and an unclassified Flavobacteriaceae (OTU 277). The two bleached treatments showed significant enrichment of OTUs in the genera *Pseudoalteromonas* (OTU 823) and *Thalassotalea* (OTU 649).

Metabolomes

Another potential driver of bacterioplankton enrichment in this study, beyond DOC concentration, was compositional differences in the DOM exudates. Untargeted metabolomics was performed to assess the impact of DOM quality on microbial community structure. The exo-metabolomes consisting of the extracted ion-chromatograms (XIC values) of each metabolite were used to generate a Bray-Curtis dissimilarity matrix to test multivariate differences between the six treatments at time point T= 0. The exo-metabolomes indicated that different treatments produced compositionally distinct DOM exudates following the three hour DOM exudation (PERMANOVA, $F=1.7847$, $R^2=0.44788$, $p\leq 0.001$) (Figure 4A). Consistent with the bacterioplankton data, coral samples clustered separately from the water negative controls and within the coral treatments, coral Controls maintained distinct metabolomes compared to the three stress treatments (one-way PERMANOVA $F=1.3799$, $R^2=0.37162$, $p=0.005$). Multivariate comparisons between the 16S rDNA and metabolomics distance matrices confirmed that DOM composition significantly correlated with bacterioplankton community structure (Procrustes correlation=0.8612, significance=0.001; Mantel $R=0.5993$, significance=0.001) (Figure 4B), indicating that bacterioplankton community changes may be a response to shifts in DOM exudate quality as well as quantity.

DISCUSSION

This study presents a comprehensive assessment of how short-term thermal stress and long-term bleaching, separately and in combination, influence reef bacterioplankton via DOM exudation. Our results indicate that thermally-induced bleaching events both increase and alter coral DOM exudation with cascading impacts on reef bacterioplankton dynamics that potentially hamper coral resistance to and recovery from bleaching.

Thermally stressed and bleaching corals release DOM that increases microbial load

Heated corals had the highest DOC fluxes of roughly $15 \mu\text{M C} \cdot (\text{dm}^2)^{-1} \cdot \text{h}^{-1}$, marking a substantial contribution to reef DOC that is between 8.4 and 13.6 times higher than previously documented coral DOC release rates in Mo'orea (Haas et al., 2011, 2013). Photosynthesis reactions, which contribute to a portion of the DOC released by corals, are sensitive to increases in temperature (Oakley et al., 2014; Ros et al., 2020) and elevated temperatures are known to speed up enzymatic reaction rates. It is possible that maintenance of intact coral-algal symbiosis in the face of elevated temperatures may lead to higher rates of carbon fixation and higher DOC release (Oakley et al., 2014). This is supported by Hillyer et al., 2017 who found that glucose, a major product of dinoflagellate-cnidarian symbiosis (Burriesci et al., 2012; Streamer et al., 1993; Whitehead & Douglas, 2003), appears to increase in thermally stressed corals.

Both Bleached and Bleached + Heated corals had lower DOC release rates that were generally similar to DOC release rates of coral Controls. Without their endosymbionts, corals are known to catabolize internal carbon stores, especially lipids, to meet their energetic demands that are no longer satisfied by photoautotrophy (Grottoli et al., 2004, 2006; Grottoli & Rodrigues, 2011; Imbs & Yakovleva, 2012; Rodrigues & Grottoli, 2007; Schoepf et al., 2021).

DOM mobilization from internal stores could yield similar DOC release compared to healthy corals, despite reduced densities of Symbiodiniaceae.

DOM exudates from Heated, Bleached, and Bleached + Heated corals appear to be labile, i.e. readily mobilized by bacterioplankton into metabolic pathways (Carlson & Hansell, 2015). In general, DOM derived from coral treatments grew more concentrated microbial communities with faster growth rates than the Negative Controls. Heated coral DOM produced higher microbial growth rates resulting in double the bacterioplankton concentrations compared to the coral Control treatment (3,000,000 cells/mL). This rapid growth of microbes on heated coral DOM could have negative impacts on corals *in situ*, where already stressed individuals are further stressed through the generation of hypoxic zones from high levels of bacterial respiration (Barott et al., 2012; Barott & Rohwer, 2012; Jorissen et al., 2016; Roach et al., 2017; Silveira et al., 2017; Smith et al., 2006). Despite the lower DOC release rates than Heated corals, both Bleached and Bleached + Heated DOM increased bacterioplankton concentrations compared to coral Controls. This suggests that changes in the composition DOM released by stressed corals may generally increase microbial growth, regardless of concentration.

DOM from stressed corals yields a conserved enrichment of copiotrophic bacterioplankton and putative pathogens

Bacterioplankton communities fed stressed coral DOM show a conserved, directional shift of microbial community structure away from bacterioplankton associated with healthy coral DOM, indicating a potential universal response of bacterioplankton coral stress, whether that be heating, bleaching, or both. Differential abundance analysis of OTUs using DESeq2 revealed that this universal stress response in bacterioplankton communities was largely driven by an enrichment of copiotrophs and putative pathogens.

The three stressed treatments were highly enriched in bacteria commonly associated with large inputs of labile organic matter, including three *Alteromonas* OTUs (OTUs 2, 195, and

734, although OTUs 2 and 195 were only significantly enriched in Bleached and Heated), one Saprospiraceae OTU (OTU 322, significantly enriched in all three treatments), and two *Pseudoalteromonas* OTUs (OTUs 1224 and 1296, significantly enriched in all three treatments). These three taxa are common copiotrophs associated with large inputs of organic matter including from algal blooms (Baumann et al., 1972; McCarren et al., 2010; Romera-Castillo et al., 2011; Shi et al., 2012; Tada et al., 2011), in controlled incubations (James et al., 2019; Nelson & Carlson, 2012; Pontiller et al., 2022), and in response to pulses of POM on coral reefs during coral spawning (Guillemette et al., 2018). The enrichment of these OTUs in all coral stress treatments suggests a universal response of corals to heating and/or bleaching that induces the release of labile organic matter which then rapidly enriches heterotrophic bacteria in the plankton.

The universal stress response in bacterioplankton communities was also driven by an enrichment of putative pathogens, specifically in the families Colwelliaceae and Pseudoalteromonadaceae. OTU 649, belonging to the genus *Thalassotalea*, was enriched in all three treatments (only significantly so in Bleached + Heated and Bleached) and shared a 100% 16S rDNA sequence identity with a *Thalassomonas* bacteria that induced severe bleaching in corals after only 24 hours (Vieira et al., 2016). *Pseudoalteromonas* OTU 823 was also highly enriched in all three stressed coral treatments (again only significantly so in Bleached + Heated and Heated) and was closely related (100% 16S rRNA identity) to *Pseudoalteromonas piratica*, which has been identified as the causative agent of the coral disease “acute *Montipora* White Syndrome” (Beurmann et al., 2017). Enrichment of putative pathogens in the stress treatments could be driven by a positive association with coral stress metabolites (Garren et al., 2014) or because stressed corals lack the production of defense molecules; in either case, the enrichment of these pathogenic taxa could be detrimental to coral health.

Although we are not aware of any studies that have examined how coral DOM alters bacterioplankton in bottle incubations, Sun et al., 2022 examined the impact of coral bleaching

on bacterioplankton in a flow through aquaria setting and corroborate many of the observations found here: copiotrophic taxa (in this case Flavobacteriaceae) increased in heated coral treatments and there is an uptick in pathogenic gene functions after seven days of heating.

Stressed corals exude compositionally distinct DOM that correlates with conserved shifts in bacterioplankton communities

One potential driver of microbial changes in this study beyond bulk DOC differences is qualitative differences in the DOM exudates. The composition of DOM has been shown to shape microbial communities in numerous systems including coral reefs (Nelson et al., 2013), the open ocean (Azam & Malfatti, 2007), and synthetic microbial consortia (Fu et al., 2020). The same patterns hold in this study; different DOM treatments yielded different microbial communities, with DOM metabolomic composition significantly correlated with microbial community structure. This suggests that changes in the quality of coral DOM exudates, not just quantity, shapes bacterioplankton communities during thermally-induced bleaching.

The four coral treatments clustered away from the two negative water controls, aligning with previous observations that corals alter water column DOM composition (Nelson et al., 2013; Quinlan et al., 2018; Wegley Kelly, et al., 2022). Importantly, there was no distinction between two negative controls, suggesting that temperature alters DOM quality indirectly via coral exudation rather than by directly acting on the water column. Within the coral treatments, the three stressed treatments clustered away from the Control corals, suggesting that stressed corals altered the quality of their DOM exudates. The consistent clustering of stressed coral treatments away from healthy coral treatments in both the microbial and metabolomics data hints at the potential release of universal stress metabolites by corals experiencing a variety of heating/bleaching regimes, leading to conserved shifts in the DOM pool and in turn conserved shifts in bacterioplankton communities. These metabolites would be present regardless of the

specific stress regime and, once exuded into the water column, would fuel the consistent growth of opportunistic families and putative pathogens. Further studies should aim to directly assess this possibility.

Bacterioplankton response to stressed coral DOM may accelerate coral decline

Our data suggest a novel, positive feedback mechanism in which thermally stressed and/or bleached corals release DOM that enriches high abundances of rapidly growing copiotrophs and putative pathogens, which can then potentially harm the coral via hypoxia due to microbial respiration or through coral disease. A similar mechanism has been observed on algae dominated reefs; high algal benthic cover quantitatively increases and qualitatively changes DOM release, which in turn fosters a more copiotrophic microbial community with higher microbial biomass and energy use (Haas et al., 2016). This process, termed “microbialization”, is part of the broader DDAM (DOM, Disease, Algae, and Microbes) negative feedback loop in which microbialization harms coral through disease (pathogens) and hypoxia (copiotrophs), further promoting algal dominance on the reef (Barott et al., 2012; Haas et al., 2016; McDole et al., 2012). In much the same mechanism as the DDAM model, corals may negatively impact their own resistance to/recovery from thermally-induced bleaching via DOM exudation and subsequent bacterioplankton enrichment.

This study did not take into account increased temperatures during microbial growth, only the impacts of DOM. Elevated temperatures could further amplify this feedback loop by increasing microbial metabolic rates, which could be an additional factor for a rapid switch to copiotrophic communities and higher microbial abundances that wasn’t observed at ambient incubations. The combination of elevated temperatures and increased DOM could also rapidly accelerate microbial respiration, resulting in more severe hypoxia than under ambient temperatures.

The ecological implications of this study can be understood by situating the four coral treatments within the context of an *in situ* reef experiencing elevated water temperatures (Figure 5). The four experimental treatments can represent four phases of thermally-induced bleaching on a coral reef, from ambient (Control) to thermally-stressed (Heated) to actively bleaching (Bleached + Heated) to recovering (Bleached). In all three of the stressed coral DOM treatments there was a marked change in DOM exudation that drove an enrichment of copiotrophs and putative pathogens in the bacterioplankton. In the above ecological interpretation of the treatments, this indicates that the aforementioned positive feedback mechanism will be present throughout various stages of a thermal anomaly, hampering both coral resistance to and recovery from bleaching via disease and hypoxia at both the onset and termination of marine heatwaves.

Importantly, the highest concentration of DOC exudate and greatest growth of bacterioplankton was in the Heated treatment. This indicates the feedback mechanism is most pronounced at the onset of coral thermal stress. Water column pathogens and copiotrophs, sniffing out and gorging on thermally stressed coral DOM exudate, may push individual corals towards more severe bleaching. If a single coral bleaches, this mechanism may have minimal impact on the water column biogeochemistry, but if an entire reef experiences elevated temperatures, the large flux of labile DOM into the water column could propagate a reef-wide shift in microbial communities that may prevent coral recovery. Additionally, coral mortality as a result of bleaching and the aforementioned mechanisms could lead to a further pulse of organic matter fuel into the water column, exacerbating the already adverse situation and turning bleaching reefs into a dead zone.

Conclusion

Assessing the effect of thermally-induced coral bleaching on water column dynamics reveals that stressed corals enrich a glut of copiotrophic, putatively pathogenic bacteria in the

408 plankton via DOM exudation. At the coral colony level these effects may reduce a corals' ability
409 to resist and recover from thermally-induced bleaching. Translated to a reef-wide scale, thermal
410 anomalies and mass bleaching events could sharply alter biogeochemistry, carbon flux,
411 microbial communities, and ecosystem health. In this dramatic positive feedback loop, DOM is
412 the herald of the change, translating shifts in coral physiology to shifts in water column
413 dynamics. At the moment, this dynamic remains unrecognized and the effects understudied. To
414 fully understand how complex coral reef ecosystems respond to marine heatwaves, producer-
415 DOM and microbe-DOM dynamics must be taken into account.

METHODS

Experimental Design

Field Collection

Coral nubbins from three different species (*Pocillopora verrucosa*, *Acropora pulchra*, and *Porites rus*) were collected in Mo'orea, French Polynesia on May 8th, 2019 immediately following a bleaching event (Figure 1B). For more on this bleaching event, temperatures of Figure 1B, and sample collection, see supplementary methods. Coral nubbins from the three species were visually inspected at the time of collection and assigned as either “unbleached” or “bleached” phenotypes. Coral bleaching status was again validated prior to the experiment with a visual inspection and assessment of Symbiodiniaceae cell densities via flow cytometry (Figure 1C).

Pre-Treatment in Flow-Through Aquaria

To mimic reef-wide bleaching/thermal stress signals, two nubbins from each of the three coral species at a given bleaching phenotype were combined with unfiltered water in individual aquaria for a total of six coral fragments in each of the 12 aquaria. Aquaria (n=3 per treatment) were exposed to seven days of either ambient (28.6 °C) or elevated water temperatures (32 °C +/- 0.2 °C) and ambient light levels. For specifications of the pumps and heaters, see supplementary methods. The combination of bleaching level and temperature yielded four treatments: “Control”, “Heated”, “Bleached”, and “Bleached + Heated” (Fig A.I and A.II). Additionally, two water-only control aquaria, one for each temperature treatment, were included (“Negative Control” and “Negative Control + Heated”).

DOM Exudation Experiment

On the day of the experiment, after seven days of pretreatment, the flow through of unfiltered water and the recirculation of water within the aquaria was stopped. Water was

removed from each aquaria until 400 mL remained (roughly $\frac{1}{3}$ of the aquaria volume). Subsequently, 800 mL 0.22 μm -filtered offshore water was then added to yield a final volume of 1200 mL. Corals were left in the aquaria to exude DOM for three hours (15:00 h - 18:00 h) while heat treatments were maintained (Fig 1.A.III). After three hours DOM exudates were collected by filtering the 1200 mL of aquaria water through a 0.22 μm PES Sterivex (Millipore) filter into acid-washed 2 L polycarbonate bottles. One of the triplicates of the “Heated” treatment was lost during this step resulting in $n=2$. To minimize DOM contamination from the filter matrix, all filters were previously flushed with 50-100 mL of 0.22 μm filtered offshore water. Following exudation corals were removed from the aquaria and airbrushed to collect tissue slurry for downstream Symbiodiniaceae quantification.

Dilution Cultures

Filtered DOM exudates were used as growth media for dark incubation dilution cultures. Unfiltered back-reef seawater collected from the LTER 1 was used as an inoculum. From each replicate aquaria 1200 mL of DOM media was mixed with 400 mL bacterioplankton inoculum (3:1 volumetric ratio) via inversion in acid washed 2 L polycarbonate bottles (Figure 1.A.IV). Dilution cultures were then split equally into two 1 L acid washed polycarbonate bottles (800 mL culture per bottle). Half of the bottles were immediately destructively sampled at the beginning of culturing (T_0 , $n=3$ per treatment), while the remaining bottles ($n=3$ per treatment) were incubated in the dark at ambient temperatures for 36 hours.

Sample Collection and Processing

Symbiodiniaceae Quantification

To assess bleaching status of the corals during collection and at the end of the seven day incubation and exudation experiment, coral nubbins were flash-frozen and airbrushed using

0.22 μ m filtered seawater. Tissue slurries were analyzed using flow cytometry following the protocol outlined in Fox et al., 2021. For details, please see supplementary methods.

Bacterioplankton Abundance

Samples for bacterioplankton abundance measurement via flow cytometry were taken throughout the dilution cultures at 0, 2, 8, 16, 20, 24, 32, and 36 hours. At every time point, 1 mL of each sample was fixed with 16 μ L of 32% paraformaldehyde PFA. Samples were run on an Attune Acoustic Focusing Cytometer (Applied Biosystems, Part No. 4445280ASR) at University of Hawai'i at Mānoa to enumerate bacterial cell counts (Nelson et al., 2015). For sample collection details and flow cytometer settings, see the supplementary methods (Figure S1).

Water Collection for Bacterial Community Composition, Dissolved Organic Carbon and Metabolite Solid Phase Extraction

At 0 and 36 h timepoints water (800 mL) was sampled for microbial communities, DOC, and solid phase extraction of DOM using a peristaltic pump connected to acid washed and seawater leached silicon tubing. Sample water (800 mL) was passed through a 0.22 μ m Sterivex to collect bacterioplankton for downstream DNA analysis.

DOC samples were taken by collecting 35 mL of 0.22 μ m sterivex filtrate in acid washed, combusted, triple sample-rinsed clear glass vials. Care was made to flush each Sterivex with ~50 mL of sample water prior to collecting DOC to avoid contamination from the filter. DOC samples were then acidified with 50 μ L of 4N hydrochloric acid to yield a pH of less than 3. The DOC samples were processed and analyzed via high-temperature combustion on slightly modified Shimadzu TOC-V analyzers at UCSB according to the protocol outlined in Carlson et al., 2010.

For analysis of metabolites, exactly 700 mL of the remaining 0.22 μ m Sterivex filtrate was collected in acid washed 1 L polycarbonate bottles and acidified with HCl to pH < 2. A small

volume (50 mL) of the acidified sample water was used to flush the lines prior to the solid phase extraction resulting in 650 mL of sample for solid phase extraction. Two bottles had less than 650 mL acidified sample water and were equalized to 500 mL solid phase extractions. The difference in volume was later corrected by the resuspension step prior to LC-MS/MS analysis. Metabolites were extracted using a 200 mg mass Bond Elut-PPL (Agilent) cartridges following Dittmar et al., 2008 and Petras et al., 2017. Detailed metabolite extraction methods and all sample handling and storage can be found in the supplementary methods.

Microbial Community DNA Extraction, Library Prep, and Sequencing

Sample DNA extraction protocols followed those outlined in Bullington et al., 2022. For details, please see supplementary methods. Library preparation of the V4 16S rRNA gene region for amplicon sequencing was conducted at the University of Hawai'i at Mānoa Microbial Genomics and Analytical Laboratory using a single barcode library preparation approach with Golay barcoded forward primers and non-barcoded reverse primers. For an overview of primers and settings used, see the supplementary methods. Amplicons were pooled and sequenced using an Illumina MiSeq V3 600 paired-end cycle run at the University of Hawai'i at Mānoa Advanced Studies in Genomics, Proteomics and Bioinformatics facility. All samples were amplified and sequenced in duplicate technical replicates. Method blanks had substantially lower sequence read depth (mean = 1,590 reads/sample) than samples (mean = 88,681), with samples ranging from 12,609 reads/sample to 155,685 reads/sample.

Dissolved Organic Matter Composition

PPL cartridges were eluted with 2 mL methanol. Extracts were dried down with a vacuum centrifuge and redissolved with 70 µL 80% methanol:water with 1% formic acid. The two samples that had less volume were redissolved to 50 µL so that all concentrations were normalized to filtrate volume. Samples were transferred into a combusted glass insert. A 10 µL

aliquot of each sample was analyzed by injection into a Vanquish ultra-high performance liquid chromatography system (UHPLC) coupled to a Q-Exactive Orbitrap Mass Spectrometer (Thermo Fisher Scientific, Bremen, Germany). Chromatographic separation was performed with a C18 core-shell column (Kinetex, 150 × 2 mm, 1.8 µm particle size, 100 Å pore size, Phenomenex, Torrance, USA) all using the settings and protocol described in Petras et al., 2017 and Wegley Kelly et al., 2022.

Data Processing and Analysis

16S Amplicon Bioinformatics

16S rRNA gene amplicon sequences were processed using the nextflow bioinformatic pipeline (version 19.10.0) outlined in Arisdakessian et al., 2020 and Jani et al., 2021. Detailed bioinformatic methods can be found in the supplementary methods. In brief, raw paired fastq reads were preprocessed using the DADA2 R package (Callahan et al., 2016a). We used mothur (Schloss et al., 2009) with the Silva (release 132) database (Quast et al., 2013) to align and annotate the sequences, respectively. Per-sample read depth was normalized to 12,000 sequences per sample. OTUs were defined as unique “amplicon sequence variants” (100% clustering OTUs) by DADA2 (Callahan et al., 2016). Lastly, we used the lulu R package to remove artefactual OTUs (Frøslev et al., 2017) and discarded OTUs represented by two or less reads across the 243 samples included in this library. UniFrac distance matrices were constructed from the OTU data and used to assess multivariate differences between microbial communities (Lozupone & Knight, 2005). At the final time point, two outlier samples were identified and removed from downstream 16S analysis (outliers were defined as samples whose log₁₀ distance from the centroid of a treatment ≥ 1.5 SD above the mean log₁₀ distance from the centroid for a given treatment).

Metabolomics Chemoinformatics

RAW files were converted to .mzML files using MSConvert (Chambers et al., 2012). MZmine3 (version 3.2.8) (Pluskal et al., 2010) was used for alignment between samples and feature extraction. In order to yield higher consensus alignment quality of MS2 spectra to improve database matching and molecular networking, the 35 samples from this experiment were combined in MzMine with 756 coral reef environmental and experimental DOM samples belonging to tandem studies conducted during the same fieldwork period at Gump Station. Detailed chemoinformatic parameters can be found in the supplemental methods. Metabolite cheminformatics generated 54,040 total metabolite ion-features (hereafter referred to as features). Ten procedural blanks (LC/MS grade water run in parallel with samples) were included in the run. These procedural blanks were used to identify background features and transient features in the 35 samples from this experiment. Background features were defined as features with an average intensity across all samples which is less than double the maximum intensity of that feature in the procedural blanks. Transient features are defined as features that do not exceed 5×10^4 extracted ion chromatogram values (XIC) in more than 2 samples. Blank correction and transient feature removal removed 29,286 and 6,483 features, respectively. This resulted in 18,271 features with XIC-values (Extracted-ion chromatogram values or peak areas) which composes what we consider the exo-metabolome (mixture of ambient and exudate features) which was used in downstream analysis.

Statistics

Data analysis and statistics were done using R (version 4.2.1). Main packages used are the core packages within tidyverse (Wickham et al., 2019), vegan (Oksanen, 2013), BiodiversityR (Kindt & Coe, 2005), pairwiseAdonis (Martinez P., 2020), and stats (R Core Team, 2013). R scripts and additional packages are available through <https://github.com/NIOZ-DOM-Analysis/ABCDom>.

570 Symbiodiniaceae cell densities and bacterioplankton cell concentrations had Gaussian
571 distributions after log10 transformation and square root transformation, respectively, and
572 treatment effects were tested using ANOVAs. Surface area normalized DOC flux for the coral
573 treatments was determined by calculating the difference in DOC concentration between each
574 treatment and their respective negative controls, normalizing this value to coral surface area
575 and dividing it by the duration of the DOC exudation period (three hours). DOC areal flux data
576 had a non-Gaussian distribution and thus treatment was tested using non-parametric Kruskal-
577 Wallis tests. PERMANOVA tests were run on weighted Unifrac dissimilarity matrices derived
578 from 16S amplicon sequencing data to test the effect of treatment on microbial community
579 structure. To assess multivariate shifts in the exo-metabolomes, the metabolite feature table
580 containing XIC data was converted to relative abundance data and used to generate a Bray-
581 Curtis dissimilarity matrix, which was then used in downstream PERMANOVA testing.

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618 WJS, MGIA, LWK, ZQ, AFH, CEN designed the study, CC, PCD, LIA, CEN, AFH, LWK

619 provided reagents and analytical tools. WJS, MGIA, ZQ, JAB performed the experiment.

620 Samples were processed by WJS, ZQ, IK, JAB, and data analysis and curation was performed

621 by WJS, MGIA, ZQ, IK. WJS, MGIA performed the formal analysis, visualization and wrote the

622 original draft. All co-authors reviewed and edited the manuscript at various stages. CEN and

623 AFH supervised the project. WJS and MGIA contributed equally.

624

625 **COMPETING INTERESTS**

626 The authors declare no competing interests.

627

628 **DATA AVAILABILITY**

629 Sequencing reads from the demultiplexed samples analyzed in this study have been deposited

630 in the NCBI Sequence Read Archive (SRA) under the BioProject accession xxxxxx (submission

631 to SRA to be finalized and made public upon acceptance). All LC-MS/MS data are publicly

632 available and deposited in the MassIVE data repository (<http://massive.ucsd.edu>) under the
633 accession number MSV000088021 (MassIVE repository made public upon acceptance).

634

635 **CODE AVAILABILITY**

636 Scripts used to analyze the data in R have been deposited in GitHub at

637 <https://github.com/NIOZ-DOM-Analysis/ABCDom> (repository made public with DOI via Zenodo

638 upon acceptance).

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