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 and significantly increased growth of bacterioplankton, enriching copiotrophs and putative pathogens. Together these results demonstrate how the impacts of both short-term thermal stress and long-term bleaching may extend into the water column, with altered coral DOM exudation driving microbial feedbacks that 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

61 enriched in genes related to chemotaxis, motility, and signal transduction, suggesting that these

62 regions surrounding corals contain bacterioplankton with the metabolic capacity to directly

63 interact with corals (Ochsenkühn et al., 2018; Silveira et al., 2017; Tout et al., 2014; Walsh et

64 al., 2017). This zone of interaction is an essential area for feedback loops between the benthos

65 and the water column in the coral reef ecosystem, as changes in bacterioplankton may

66 influence coral physiology (Barott et al., 2012). Despite the burgeoning knowledge of how

67 healthy corals influence bacterioplankton via DOM exudation, relatively little is known about if

68 and how this relationship changes when corals are stressed.

69   One major stressor corals experience is ocean warming, with marine heatwaves

70 occurring more frequently due to global climate change (Arias et al., 2021; Cooley et al., 2022;

71 Levitus et al., 2012). Thermal stress harms corals via bleaching, a well-documented and

72 widespread phenomenon in which the symbiosis between corals and Symbiodinacaeae breaks

73 down as corals are exposed to elevated temperatures for an extended period of time (Brown,

74 1997). Mass coral bleaching has been recorded since 1979 and has increased in frequency,

75 with a 3-fold increase in bleaching events in 2006-2012 compared to 1985-1991, restricting the

76 time for coral reefs to recover between bleaching events (Cooley et al., 2022; Heron et al.,

77 2016; van Hooidonk et al., 2016). Although corals can recover from bleaching, they will die if

78 thermal stress persists (Hoegh-Guldberg, 1999). Even at sub-lethal levels, coral bleaching alters

79 the coral holobiont's metabolism (Innis et al., 2021), its chemistry (Roach et al., 2021), and

80 microbiota (Bourne et al., 2016; Liang et al., 2022; Littman et al., 2011; McDevitt-Irwin et al.,

81 2017; Oppen & Blackall, 2019; Thurber et al., 2009).

82   Recent research suggests that coral-water column interactions are altered during

83 periods of elevated temperatures (Garren et al., 2014; Niggl et al., 2009; Tremblay et al., 2012).

84 Niggl *et al.* (2009) found that bleaching corals released elevated levels of particulate nitrogen

85 (PN) and particulate organic carbon (POC) into the water column. In another study, heated

86 *Stylophora pistillata* corals showed a change in total organic carbon (TOC) flux direction,

87   transitioning from negative flux in healthy corals (uptake) to positive flux in heated/bleached

88   corals (release) (Tremblay et al., 2012). These alterations to water column chemistry likely shift

89   the bacterioplankton community composition as specific taxa respond to metabolites released

90   by stressed corals. In one study, the bacterial pathogen *Vibrio coralliilyticus* responded to DMSP

91   as a chemotactic cue when it was released at elevated concentrations by heat stressed coral

92   (Garren et al., 2014). Even under ambient conditions, coral mucus elicits a rapid chemokinetic

93   and transcriptional response in *Vibrio coralliilyticus*, further suggesting that this pathogen uses

94   coral chemical cues to trace and target its host (Gao et al., 2021). Given that healthy corals

95   exude DOM into the surrounding seawater and influence subsequent bacterioplankton

96   dynamics, we hypothesized that 1) thermal stress and bleaching can dramatically alter DOC

97   exudation rates and DOM composition with cascading effects on bacterioplankton growth and

98   community structure and 2) short-term thermal stress and long-term bleaching will have different

99   effects. These different effects will help elucidate how the succession of bleaching, from onset

100   to recovery or death, influences the succession of DOM and bacterioplankton *in situ*.

101

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 six 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) with unfiltered water sourced from a depth of 6 m directly adjacent to the Gump Station fringing reef (Fig 1A.I). Rather than test for species-specific differences in DOM release and bacterioplankton response, we opted to combine the 3 coral species in individual aquaria to mimic the natural composition of coral communities on Mo'orea (Edmunds, 2022) and assess the general coral community response to thermal stress and bleaching. 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, the water was changed to filtered (0.22 μm) seawater and corals were left to exude DOM for 3 hours. Coral community 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%

128   acid-washed, triple milliQ rinsed (hereafter termed "acid washed") polycarbonate bottles in the

129   dark at ambient temperatures for 36 hours and sampled at the beginning (n=3 per treatment)

130   and end (n=3 per treatment) of the incubation. We used a combination of bulk DOC

131   measurements, flow cytometry, 16S amplicon sequencing, and untargeted metabolomics to

132   assess differences in the composition of DOM exudates and how these exudates altered

133   microbial growth and community structure (Fig 1 A.V).

134

135   **Symbiodiniaceae Densities**

136   Symbiodiniaceae cell densities were used to assess individual and aquaria-wide

137   bleaching levels of corals collected in the field and after the seven day pre-treatment,

138   respectively. At collection, bleached corals had significantly lower Symbiodiniaceae cell

139   densities (two-way ANOVA, $F=45.552$, $p=2.67e-08$). Coral species also had a significant effect

140   on Symbiodiniaceae densities (two-way ANOVA, $F=4.738$, $p=0.0137$), as well as the interaction

141   between coral species and bleaching (two-way ANOVA, $F=4.287$, $p=0.0199$) (Figure 1C).

142   After seven days of incubation at ambient and elevated temperatures, the average

143   Symbiodinaceae densities showed that the four coral treatments had varying degrees of

144   bleaching (Figure 1D). Bleached corals had significantly lower Symbiodinaceae densities (two-

145   way ANOVA, $F=6.584$, $p=0.0333$). Heating did not have a significant effect on Symbiodiniaceae

146   cell densities ($F=0.001$, $p=0.9727$), and neither did the interaction between heating and

147   bleaching (two-way ANOVA, $F=1.284$, $p=0.2901$). Therefore the Control treatment had the

148   highest Symbiodiniaceae densities during the exudation experiment. Heated aquaria exhibited

149   slightly lower Symbiodiniaceae cell densities consistent with some paling, yet still had higher cell

150   densities than their Bleached and Bleached + Heated counterparts.

151

152   **Dissolved Organic Carbon**

153   Control corals exuded roughly 5 µM C·$(dm^2)^{-1}·h^{-1}$ while Heated corals and Bleached

154   corals exhibited roughly 289% (mean 13.22 µM C·$(dm^2)^{-1}·h^{-1}$) and 177% (mean 8.10 µM

155   C·$(dm^2)^{-1}·h^{-1}$) higher DOC fluxes. Bleached + Heated corals exhibited undetectable DOC flux.

156   Although DOC exudation appeared to be affected by treatment, we were unable to elucidate

157   significant differences in areal DOC flux rates possibly due to small sample size and short

158   exudation times (Kruskal-Wallis chi-squared=4.1667, p=0.244) (Figure 2A). Coral treatments

159   generally had higher raw DOC concentrations than the water controls, although this effect was

160   not significant (Kruskal-Wallis chi-squared=9.3187, p=.09) (Figure S2).

161

162   **Microbial Growth**

163   Flow cytometry revealed distinct microbial growth patterns between the DOM

164   treatments. Two-way ANOVAs were used to test the effect of both timepoint and treatment on

165   bacterioplankton cell concentrations, We found that bacterioplankton concentrations significantly

166   increased through time in the dark bottle incubations (two-way ANOVA, F=104.372, p<2.2E-16)

167   and differed significantly between treatments (two-way ANOVA, F=53.685, p<2.2E-16) (Figure

168   2B). All coral treatments had significantly higher cell concentrations than both the Negative

169   Control and the Negative Control + Heated (Tukey post-hoc test, p<0.05). Within the coral DOM

170   treatments, Heated exudates yielded significantly higher bacterioplankton concentrations than

171   the Control (Tukey post-hoc test, p<0.05), with bacterioplankton grown on Heated DOM

172   reaching concentrations of 3,160,000 cells/mL (± 790,000), nearly double that of the Control

173   (1,562,000 cells/mL ± 137,000) (Figure 2B). Bacterioplankton specific growth rate also differed

174   significantly between the treatments (one-way ANOVA, F=6.363, p=0.005) (Figure S3).

175

176   **Microbial Community Structure**

7

177   The DOM derived from the six treatments yielded distinct microbial communities after 36

178   hours of growth. There was a significant change in microbial communities from the start to the

179   end of the bottle incubations, indicating that communities changed through the bottle incubation

180   and were not simply reflective of the starting communities (PERMANOVA, F=72.033, R^2=0.71,

181   p≤.001, Figure S4). After 36h, bacterioplankton grown on coral exudates were significantly

182   different from those grown on water negative controls (PERMANOVA F=8.679, R^2=0.40,

183   p≤.001), and overall DOM treatment had a significant effect on microbial community structure

184   (PERMANOVA F=4.637, R^2=0.72, p≤.001) (Figure 3A). Within the coral treatments, Controls

185   maintained distinct community structure from the Heated, Bleached, and Bleached + Heated

186   communities, hereafter collectively referred to as "stressed" (PERMANOVA F=2.822, R^2=0.59,

187   p=0.009). There was overlap within the stressed communities and a consistent shift in

188   ordination space away from the Controls, indicating a potentially conserved change that occurs

189   in microbial communities in response to stressed coral exudates.

190   Many eutrophic coastal-associated bacterial families were overrepresented in the

191   negative controls including Nitrincolaceae and Methylophagaceae (Francis et al., 2021), as well

192   as the common coral reef associated family Rhodobacteraceae (Apprill et al., 2021; Comstock

193   et al., 2022; Haas et al., 2016; Kelly et al., 2019; Nelson et al., 2011). Coral DOM microbial

194   communities were dominated by the families Alteromonadaceae and Rhodobacteraceae,

195   although there was substantial variation between the four treatments (Figure 3B, Table S1).

196   Control corals maintained distinct microbial communities from both negative controls and

197   stressed corals, overrepresented in the families Cryomorphaceae, Litoricolaceae, and

198   Halieaceae. Alteramonadaceae, a common marine copiotrophic family (Baumann et al., 1972),

199   was lowest in communities grown on Control exudates (28.3%) and substantially higher in the

200   communities growing on the stressed coral exudates (46.6%-38.6%). Pseudoalteromonadaceae

201   also increased in abundance from Control communities to stressed communities (3.3% in

202   Control, and a mean of 9.1% in stressed). The common coral reef-associated family

203   Rhodobacteraceae was higher in the Control (21.3%) and lower in the three stressed treatments

204   (13.7%-19.4%). Another common coral reef associated family, Cryomorphaceae, was abundant

205   in the Control treatment (13.0%) and then reduced in abundance in the stressed treatments

206   (5.6%-7.2%). Microbial community alpha diversity metrics (observed sequences, Chao diversity,

207   Shannon diversity, and Shannon's Evenness) were assessed after 36 hours of growth (Figure

208   S5), with none of these indices being significantly affected by treatment (one-way ANOVA,

209     $p \geq .05$).

210

211   **<u>Bacterial Taxa Differential Abundance Analysis</u>**

212   Multivariate analysis demonstrated that stressed corals enriched distinct

213   bacterioplankton communities compared to their Control counterparts. In order to directly

214   elucidate which specific bacterial taxa were driving these differences, we performed DESeq2,

215   (see supplementary methods) on a subset of the data that only included the four coral DOM

216   treatments (Love et al., 2014), yielding a final count of 159 OTUs to be run through DESeq2.

217   The log2 fold-change of OTU abundances was calculated between the three coral stress

218   treatments and the coral controls to elucidate OTUs that were differentially abundant when

219   corals were bleached and/or heated (Table S2) (Figures 3C and S6).

220   A total of 31 significantly differentially abundant bacterial OTUs (19.5%) were identified

221   by DESeq2 (DESeq2, log2 fold-change>0, $p \leq .05$ after FDR adjustment, Table 1, Figures 3C,

222   S6, and S7). These OTUs belonged to four bacterial and one archaeal class:

223   Alphaproteobacteria, Gammaproteobacteria, Bacteroidia, Deltaproteobacteria, and

224   Thermoplasmata, with the majority (64.5%) of differentially abundant OTUs belonging to

225   Gammaproteobacteria. Within Gammaproteobacteria, there was a significant enrichment of

226   numerous abundant Alteromonadaceae and Pseudoalteromonadaceae OTUs in at least one of

227   the three treatments (75% of all differentially abundant Gammaproteobacteria OTUs).

228   In all three stress treatments there was a significant enrichment of two

229   *Pseudoalteromonas* OTUs (1224 and 1296), one *Alteromonas* OTU (734), and one unclassified

230   Saprospiraceae OTU (322). All three stress treatments also showed an enrichment of a highly

231   abundant *Alteromonas* OTU (2), although this was only statistically significant in the Bleached

232   and Heated treatments. There were 12 differentially abundant OTUs found only to be significant

233   in the Bleached treatment including significant enrichment in members of the genus

234   *Psuedoalteromonas* (OTUs 75 and 85), unclassified Saprospiraceae (OTU 101), and

235   *Phaeocystidibacter* (OTU 480), and significant reductions in members of the genus *Litoricola*

236   OTUs 27 and 419) and unclassified Alteromonadaceae (OTUs 368, 1012, and 1023). The two

237   heated treatments had significant enrichment in OTUs of the genus *Psuedoalteromonas* (OTU

238   853), *Aestuariibacter* (OTU 48), and an unclassified Flavobacteriaceae (OTU 277). The two

239   bleached treatments showed significant enrichment of OTUs in the genera *Pseudoalteromonas*

240   (OTU 823) and *Thalassotalea* (OTU 649). Visualization of pairwise co-occurrence patterns of

241   OTUs from the final time point reinforces these conclusions (Figure S8). OTUs enriched in the

242   coral stress treatments including Alteromonadaceae, Pseudoalteromonadaceae, and

243   Saprospiraceae clustered together in the upper portion of the network and showed a high

244   degree of connectivity with each other (i.e. OTU 1224 and OTU 75), yet limited significant

245   positive correlations with OTUs in the network that were enriched in coral controls and/or

246   negative water controls.

247

248   **<u>Metabolomes</u>**

249   Another potential driver of bacterioplankton enrichment in this study, beyond DOC

250   concentration, was compositional differences in the DOM exudates. Untargeted metabolomics

251   was performed to assess the impact of DOM quality on microbial community structure. The exo-

252   metabolomes consisting of the extracted ion-chromatograms (XIC values) of each metabolite

253   were used to generate a Bray-Curtis dissimilarity matrix to test multivariate differences between

254   the six treatments at time point T= 0. The exo-metabolomes indicated that different treatments

255   produced compositionally distinct DOM exudates following the three hour DOM exudation

256   (PERMANOVA, F=1.7847, R^2=0.44788, p≤.001) (Figure 4A). Consistent with the

257   bacterioplankton data, coral samples clustered separately from the water negative controls and

258   within the coral treatments, coral Controls maintained distinct metabolomes compared to the

259   three stress treatments (one-way PERMANOVA F=1.3799, R^2=0.37162, p=0.005). Multivariate

260   comparisons between the 16S rDNA and metabolomics distance matrices confirmed that DOM

261   composition significantly correlated with bacterioplankton community structure (Procrustes

262   correlation=0.8612, significance=0.001; Mantel R=0.5993, significance=0.001) (Figure 4B),

263   indicating that bacterioplankton community changes may be a response to shifts in DOM

264   exudate quality as well as quantity.

265

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 by coral communities. Our results indicate that thermally-induced bleaching events both increase and alter coral community 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 μM C·$(dm^2)^{-1}$·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 not significantly different 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).

291   DOM mobilization from internal stores could yield similar DOC release compared to healthy

292   corals, despite reduced densities of Symbiodiniaceae.

293   DOM exudates from Heated, Bleached, and Bleached + Heated corals appear to be

294   labile, i.e. readily mobilized by bacterioplankton into metabolic pathways (Carlson & Hansell,

295   2015). In general, DOM derived from coral treatments grew more concentrated microbial

296   communities with faster growth rates than the Negative Controls. Heated coral DOM produced

297   higher microbial growth rates resulting in double the bacterioplankton concentrations compared

298   to the coral Control treatment (3,000,000 cells/mL). This rapid growth of microbes on heated

299   coral DOM could have negative impacts on corals *in situ*, where already stressed individuals are

300   further stressed through the generation of hypoxic zones from high levels of bacterial respiration

301   (Barott et al., 2012; Barott & Rohwer, 2012; Jorissen et al., 2016; Roach et al., 2017; Silveira et

302   al., 2017; Smith et al., 2006). Despite the lower DOC release rates than Heated corals, both

303   Bleached and Bleached + Heated DOM increased bacterioplankton concentrations compared to

304   coral Controls. This suggests that changes in the composition DOM released by stressed corals

305   may generally increase microbial growth, regardless of concentration.

306

307   **<u>DOM from stressed corals yields a conserved enrichment of copiotrophic</u>**

308   **<u>bacterioplankton and putative pathogens</u>**

309   Bacterioplankton communities fed stressed coral DOM show a conserved, directional

310   shift of microbial community structure away from bacterioplankton associated with healthy coral

311   DOM, indicating a potential universal response of bacterioplankton coral stress, whether that be

312   heating, bleaching, or both. Differential abundance analysis of OTUs using DESeq2 revealed

313   that this universal stress response in bacterioplankton communities was largely driven by an

314   enrichment of copiotrophs and putative pathogens.

315   The three stressed treatments were highly enriched in bacteria commonly associated

316   with large inputs of labile organic matter, including three *Alteromonas* OTUs (OTUs 2, 195, and

317   734, although OTUs 2 and 195 were only significantly enriched in Bleached and Heated), one

318   Saprospiraceae OTU (OTU 322, significantly enriched in all three treatments), and two

319   *Pseudoalteromonas* OTUs (OTUs 1224 and 1296, significantly enriched in all three treatments).

320   These three taxa are common copiotrophs associated with large inputs of organic matter

321   including from algal blooms (Baumann et al., 1972; McCarren et al., 2010; Romera-Castillo et

322   al., 2011; Shi et al., 2012; Tada et al., 2011), in controlled incubations (James et al., 2019;

323   Nelson & Carlson, 2012; Pontiller et al., 2022), and in response to pulses of POM on coral reefs

324   during coral spawning (Guillemette et al., 2018). The enrichment of these OTUs in all coral

325   stress treatments suggests a universal response of corals to heating and/or bleaching that

326   induces the release of labile organic matter which then rapidly enriches heterotrophic bacteria in

327   the plankton. Through the lens of *r*- and *K*-selection, the release of surplus labile organic matter

328   by stressed corals proliferates *r*- selected copiotrophs that rapidly outcompete the *K*- selected

329   taxa that are often associated with marine oligotrophic, and specifically coral reef, systems.

330   The universal stress response in bacterioplankton communities was also driven by an

331   enrichment of putative pathogens, specifically in the families Colwellieaceae and

332   Pseudoalteromonadaceae. OTU 649, belonging to the genus *Thalassotalea*, was enriched in all

333   three treatments (only significantly so in Bleached + Heated and Bleached) and shared a 100%

334   16S rDNA sequence identity with a *Thalassomonas* bacteria that induced severe bleaching in

335   corals after only 24 hours (Vieira et al., 2016). *Pseudoalteromonas* OTU 823 was also highly

336   enriched in all three stressed coral treatments (again only significantly so in Bleached + Heated

337   and Heated) and was closely related (100% 16S rRNA identity) to *Pseudoalteromonas piratica*,

338   which has been identified as the causative agent of the coral disease "acute *Montipora* White

339   Syndrome" (Beurmann et al., 2017). Enrichment of putative pathogens in the stress treatments

340   could be driven by a positive association with coral stress metabolites (Garren et al., 2014) or

341   because stressed corals lack the production of defense molecules; in either case, the

342   enrichment of these pathogenic taxa could be detrimental to coral health.

343   Although we are not aware of any studies that have examined how <mark>stressed</mark> coral DOM

344   alters bacterioplankton in bottle incubations, Sun et al., 2022 examined the impact of coral

345   bleaching on bacterioplankton in a flow through aquaria setting and corroborate many of the

346   observations found here: copiotrophic taxa (in this case Flavobacteriaceae) increased in heated

347   coral treatments and there is an uptick in pathogenic gene functions after seven days of heating.

348

349   **Stressed corals exude compositionally distinct DOM that correlates with conserved**

350   **shifts in bacterioplankton communities**

351   One potential driver of microbial changes in this study beyond bulk DOC differences `

352   is qualitative differences in the DOM exudates. The composition of DOM has been

353   shown to shape microbial communities in numerous systems including coral reefs (Nelson et al.,

354   2013), the open ocean (Azam & Malfatti, 2007), and synthetic microbial consortia (Fu et al.,

355   2020). The same patterns hold in this study; different DOM treatments yielded different

356   microbial communities, with DOM metabolomic composition significantly correlated with

357   microbial community structure. This suggests that changes in the quality of coral DOM

358   exudates, not just quantity, shapes bacterioplankton communities during thermally-induced

359   bleaching.

360   The four coral treatments clustered away from the two negative water controls, aligning

361   with previous observations that corals alter water column DOM composition (Nelson et al.,

362   2013; Quinlan et al., 2018; Wegley Kelly, et al., 2022). Importantly, there was no distinction

363   between two negative controls, suggesting that temperature alters DOM quality indirectly via

364   coral exudation rather than by directly acting on the water column. Within the coral treatments,

365   the three stressed treatments clustered away from the Control corals, suggesting that stressed

366   corals altered the quality of their DOM exudates. The consistent clustering of stressed coral

367   treatments away from healthy coral treatments in both the microbial and metabolomics data

368   hints at the potential release of universal stress metabolites by corals experiencing a variety of

369 heating/bleaching regimes, leading to conserved shifts in the DOM pool and in turn conserved

370 shifts in bacterioplankton communities. These metabolites would be present regardless of the

371 specific stress regime and, once exuded into the water column, would fuel the consistent growth

372 of opportunistic families and putative pathogens. Further studies should aim to directly assess

373 this possibility.

374 In this study we used a mixture of three common Mo'orea coral species in each aquaria

375 in order to investigate the coral community DOM exudation response to thermal

376 stress/bleaching. Different coral species can exude different DOM quantities and compositions

377 and yield slightly different microbial communities, although differences between coral species

378 are smaller than differences between broader benthic "guilds" (Nelson et al., 2013; Wegley Kelly

379 et al., 2022). The current setup does not allow us to investigate the species specific response to

380 heating and bleaching. While we hypothesize that the response of increased and altered DOM

381 exudation is a universal response on heating and bleaching by coral communities, future studies

382 should investigate species specific differences. If there are substantial differences in DOM

383 exudation and subsequent bacterioplankton growth between coral species, then the

384 composition of the reef benthos might influence the reef-wide ecological impact and response

385 on thermal and bleaching stress or its recovery.

386

387 **Bacterioplankton response to stressed coral DOM may accelerate coral decline**

388 Our data suggest a novel, positive feedback mechanism in which thermally stressed

389 and/or bleached corals release DOM that enriches high abundances of rapidly growing

390 copiotrophs and putative pathogens, which can then potentially harm the coral via hypoxia due

391 to microbial respiration or through coral disease. A similar mechanism has been observed on

392 algae dominated reefs; high algal benthic cover quantitatively increases and qualitatively

393 changes DOM release, which in turn fosters a more copiotrophic microbial community with

394 higher microbial biomass and energy use (Haas et al., 2016)**.** This process, termed

395 "microbialization", is part of the broader DDAM (DOM, Disease, Algae, and Microbes) negative

396 feedback loop in which microbialization harms coral through disease (pathogens) and hypoxia

397 (copiotrophs), further promoting algal dominance on the reef (Barott et al., 2012b; Haas et al.,

398 2016; McDole et al., 2012). In much the same mechanism as the DDAM model, corals may

399 negatively impact their own resistance to/recovery from thermally-induced bleaching via DOM

400 exudation and subsequent bacterioplankton enrichment.

401   This study used a sealed, controlled bottle system to accurately measure DOC and

402 microbial growth characteristics. However, *in situ* conditions are vastly different from bottles or

403 flow through mesocosms; physical dynamics like reef depth, water flow, and residence time, as

404 well as the relative abundance of specific coral species on a reef, all likely impact the degree to

405 which our observed findings translate to *in situ* impacts.

406   This study did not take into account increased temperatures during microbial growth,

407 only the impacts of DOM. Elevated temperatures could further amplify this feedback loop by

408 increasing microbial metabolic rates, which could be an additional factor for a rapid switch to

409 copiotrophic communities and higher microbial abundances that wasn't observed at ambient

410 incubations. The combination of elevated temperatures and increased DOM could also rapidly

411 accelerate microbial respiration, resulting in more severe hypoxia than under ambient

412 temperatures.

413   The ecological implications of this study can be understood by situating the four coral

414 treatments within the context of an *in situ* reef experiencing elevated water temperatures (Figure

415 5). The four experimental treatments can represent four phases of thermally-induced bleaching

416 on a coral reef, from ambient (Control) to thermally-stressed (Heated) to actively bleaching

417 (Bleached + Heated) to recovering (Bleached). In all three of the stressed coral DOM treatments

418 there was a marked change in DOM exudation that drove an enrichment of copiotrophs and

419 putative pathogens in the bacterioplankton. In the above ecological interpretation of the

420 treatments, this indicates that the aforementioned positive feedback mechanism will be present

421 throughout various stages of a thermal anomaly, hampering both coral resistance to and

422 recovery from bleaching via disease and hypoxia at both the onset and termination of marine

423 heatwaves.

424   Importantly, the highest concentration of DOC exudate and greatest growth of

425 bacterioplankton was in the Heated treatment. This indicates the feedback mechanism is most

426 pronounced at the onset of coral thermal stress. Water column pathogens and copiotrophs,

427 sniffing out and gorging on thermally stressed coral DOM exudate, may push individual corals

428 towards more severe bleaching. If a single coral bleaches, this mechanism may have minimal

429 impact on the water column biogeochemistry, but if an entire reef experiences elevated

430 temperatures, the large flux of labile DOM into the water column could propagate a reef-wide

431 shift in microbial communities that may prevent coral recovery. Additionally, coral mortality as a

432 result of bleaching and the aforementioned mechanisms could lead to a further pulse of organic

433 matter fuel into the water column, exacerbating the already adverse situation and turning

434 bleaching reefs into a dead zone.

435

436 **Conclusion**

437   Assessing the effect of thermally-induced coral bleaching on water column dynamics

438 reveals that stressed corals enrich a glut of copiotrophic, putatively pathogenic bacteria in the

439 plankton via DOM exudation. Based on these results we hypothesize that at the coral colony

440 level these effects may reduce a corals' ability to resist and recover from thermally-induced

441 bleaching. When our results are translated to a reef-wide scale, we predict that thermal

442 anomalies and mass bleaching events could sharply alter reef water biogeochemistry, carbon

443 flux, microbial communities, ecosystem health. In this dramatic positive feedback loop, DOM is

444 the herald of the change, translating shifts in coral physiology to shifts in water column

445 dynamics. At the moment, this dynamic remains unrecognized and the effects understudied. To

446 fully understand how complex coral reef ecosystems respond to marine heatwaves, producer-

447 DOM and microbe-DOM dynamics must be taken into account.

448

449 **METHODS**

450 **Experimental Design**

451 *Field Collection*

452   Coral nubbins from three different species (*Pocillopora verrucosa*, *Acropora pulchra*, and

453 *Porites rus)* were collected in Mo'orea, French Polynesia on May 8th, 2019 immediately

454 following a bleaching event (Figure 1B). For more on this bleaching event, temperatures of

455 Figure 1B, and sample collection, see supplementary methods. Coral nubbins from the three

456 species were visually inspected at the time of collection and assigned as either "unbleached" or

457 "bleached" phenotypes. After collection, corals were transported to the Gump Station research

458 facility and acclimated to ambient conditions in a water table for three days. Coral bleaching

459 status was again validated prior to the experiment with a visual inspection and assessment of

460 Symbiodiniaceae cell densities via flow cytometry (Figure 1C).

461

462 *Pre-Treatment in Flow-Through Aquaria*

463   To mimic reef-wide bleaching/thermal stress signals, two nubbins from each of the three

464 coral species at a given bleaching phenotype were combined with unfiltered water in individual

465 aquaria for a total of six coral fragments in each of the 12 aquaria. Aquaria (n=3 per treatment)

466 were exposed to six days of either ambient (28.6 °C) or elevated water temperatures (32 °C +/-

467 0.2 °C) and ambient light levels (Table S3). For specifications of the pumps and heaters, see

468 supplementary methods. The combination of bleaching level and temperature yielded four

469 treatments: "Control", "Heated", "Bleached", and "Bleached + Heated" (Fig A.I and A.II).

470 Additionally, two water-only control aquaria, one for each temperature treatment, were included

471 ("Negative Control" and "Negative Control + Heated").

472

473 *DOM Exudation Experiment*

474   On the day of the experiment, after seven days of pretreatment, the flow through of

475   unfiltered water and the recirculation of water within the aquaria was stopped. Water was

476   removed from each aquaria until 400 mL remained (roughly ⅓ of the aquaria volume).

477   Subsequently, 800 mL 0.22 µm-filtered offshore water was then added to yield a final volume of

478   1200 mL. Corals were left in the aquaria to exude DOM for three hours (15:00 h - 18:00 h) while

479   heat treatments were maintained (Fig 1.A.III). After three hours coral community DOM exudates

480   were collected by filtering the 1200 mL of aquaria water through a 0.22 µm PES Sterivex

481   (Millipore) filter into acid-washed 2 L polycarbonate bottles. One of the triplicates of the "Heated"

482   treatment was lost during this step resulting in n=2. To minimize DOM contamination from the

483   filter matrix, all filters were previously flushed with 50-100 mL of 0.22 µm filtered offshore water.

484   Following exudation corals were removed from the aquaria and airbrushed to collect tissue

485   slurry for downstream Symbiodiniaceae quantification.

486

487   *Dilution Cultures*

488   Filtered DOM exudates were used as growth media for dark incubation dilution cultures.

489   Unfiltered back-reef seawater collected from the LTER 1 was used as an inoculum. From each

490   replicate aquaria 1200 mL of DOM media was mixed with 400 mL bacterioplankton inoculum

491   (3:1 volumetric ratio) via inversion in acid washed 2 L polycarbonate bottles (Figure 1.A.IV).

492   Dilution cultures were then split equally into two 1 L acid washed polycarbonate bottles (800 mL

493   culture per bottle). Half of the bottles were immediately destructively sampled at the beginning

494   of culturing (T0, n=3 per treatment), while the remaining bottles (n=3 per treatment) were

495   incubated in the dark at ambient temperatures for 36 hours.

496

497   **Sample Collection and Processing**

498   *Symbiodiniaceae Quantification*

499   To assess bleaching status of the corals during collection and at the end of the seven

500 day incubation and exudation experiment, coral nubbins were flash-frozen and airbrushed using

501 0.22 µm filtered seawater. Tissue slurries were analyzed using flow cytometry following the

502 protocol outlined in Fox et al., 2021. For details, please see supplementary methods (Fig S1).

503

504 *Bacterioplankton Abundance*

505   Samples for bacterioplankton abundance measurement via flow cytometry were taken

506 throughout the dilution cultures at 0, 2, 8, 16, 20, 24, 32, and 36 hours. At every time point, 1 mL

507 of each sample was fixed with 16 µL of 32% paraformaldehyde PFA. Samples were run on an

508 Attune Acoustic Focusing Cytometer (Applied Biosystems, Part No. 4445280ASR) at University

509 of Hawaiʻi at Mānoa to enumerate bacterial cell counts (Nelson et al., 2015). For sample

510 collection details and flow cytometer settings, see the supplementary methods (Figure S1).

511

512 *Water Collection for Bacterial Community Composition, Dissolved Organic Carbon and*

513 *Metabolite Solid Phase Extraction*

514   At 0 and 36 h timepoints water (800 mL) was sampled for microbial communities, DOC,

515 and solid phase extraction of DOM using a peristaltic pump connected to acid washed and

516 seawater leached silicon tubing. Sample water (800 mL) was passed through a 0.22 µm

517 Sterivex to collect bacterioplankton for downstream DNA analysis.

518   DOC samples were taken by collecting 35 mL of 0.22µm sterivex filtrate in acid washed,

519 combusted, triple sample-rinsed clear glass vials. Care was made to flush each Sterivex with

520 ~50 mL of sample water prior to collecting DOC to avoid contamination from the filter. DOC

521 samples were then acidified with 50 µL of 4N hydrochloric acid to yield a pH of less than 3. The

522 DOC samples were processed and analyzed via high-temperature combustion on slightly

523 modified Shimadzu TOC-V analyzers at UCSB according to the protocol outlined in Carlson et

524 al., 2010.

525   For analysis of metabolites, exactly 700 mL of the remaining 0.22 µm Sterivex filtrate

526   was collected in acid washed 1 L polycarbonate bottles and acidified with HCl to pH < 2. A small

527   volume (50 mL) of the acidified sample water was used to flush the lines prior to the solid phase

528   extraction resulting in 650 mL of sample for solid phase extraction. Two bottles had less than

529   650 mL acidified sample water and were equalized to 500 mL solid phase extractions. The

530   difference in volume was later corrected by the resuspension step prior to LC-MS/MS analysis.

531   Metabolites were extracted using a 200 mg mass Bond Elut-PPL (Agilent) cartridges following

532   Dittmar et al., 2008 and Petras et al., 2017. Detailed metabolite extraction methods and all

533   sample handling and storage can be found in the supplementary methods.

534

535   *Microbial Community DNA Extraction, Library Prep, and Sequencing*

536   Sample DNA extraction protocols followed those outlined in Bullington et al., 2022. For

537   details, please see supplementary methods. Library preparation of the V4 16S rRNA gene

538   region for amplicon sequencing was conducted at the University of Hawaiʻi at Mānoa Microbial

539   Genomics and Analytical Laboratory using a single barcode library preparation approach with

540   Golay barcoded forward primers and non-barcoded reverse primers. For an overview of primers

541   and settings used, see the supplementary methods. Amplicons were pooled and sequenced

542   using an Illumina MiSeq V3 600 paired-end cycle run at the University of Hawaiʻi at Mānoa

543   Advanced Studies in Genomics, Proteomics and Bioinformatics facility. A total of 243 samples

544   from this experiment as well as other experiments that occurred at the same field site and time

545   were included in this sequencing library. All samples were amplified and sequenced in duplicate

546   technical replicates. Method blanks had substantially lower sequence read depth (mean = 1,590

547   reads/sample) than samples (mean = 88,681), with samples ranging from 12,609 reads/sample

548   to 155,685 reads/sample.

549

550   *Dissolved Organic Matter Composition*

551   PPL cartridges were eluted with 2 mL methanol. Extracts were dried down with a

552   vacuum centrifuge and redissolved with 70 μL 80% methanol:water with 1% formic acid. The

553   two samples that had less volume were redissolved to 50 μL so that all concentrations were

554   normalized to filtrate volume. Samples were transferred into a combusted glass insert. A 10 μL

555   aliquot of each sample was analyzed by injection into a Vanquish ultra-high performance liquid

556   chromatography system (UHPLC) coupled to a Q-Exactive Orbitrap Mass Spectrometer

557   (Thermo Fisher Scientific, Bremen, Germany). Chromatographic separation was performed with

558   a C18 core-shell column (Kinetex, 150 × 2 mm, 1.8 μm particle size, 100 Å pore size,

559   Phenomenex, Torrance, USA) all using the settings and protocol described in Petras et al.,

560   2017 and Wegley Kelly et al., 2022.

561

562   **Data Processing and Analysis**

563   *16S Amplicon Bioinformatics*

564   16S rRNA gene amplicon sequences were processed using the nextflow bioinformatic

565   pipeline (version 19.10.0) outlined in Arisdakessian et al., 2020 and Jani et al., 2021. Detailed

566   bioinformatic methods can be found in the supplementary methods. In brief, raw paired fastq

567   reads were preprocessed using the DADA2 R package (Callahan et al., 2016a). We used

568   mothur (Schloss et al., 2009) with the Silva (release 132) database (Quast et al., 2013) to align

569   and annotate the sequences, respectively. Per-sample read depth was normalized to 12,000

570   sequences per sample. OTUs were defined as unique "amplicon sequence variants" (100%

571   clustering OTUs) by DADA2 (Callahan et al., 2016). Lastly, we used the lulu R package to

572   remove artefactual OTUs (Frøslev et al., 2017) and discarded OTUs represented by two or less

573   reads across the 243 samples included in this library. UniFrac distance matrices were

574   constructed from the OTU data and used to assess multivariate differences between microbial

575   communities (Lozupone & Knight, 2005). At the final time point, two outlier samples were

576   identified and removed from downstream 16S analysis (outliers were defined as samples whose

577   log10 distance from the centroid of a treatment ≥ 1.5 SD above the mean log10 distance from

578   the centroid for a given treatment).

579

580   *Metabolomics Chemoinformatics*

581   RAW files were converted to .mzML files using MSConvert (Chambers et al., 2012).

582   MZmine3 (version 3.2.8) (Pluskal et al., 2010) was used for alignment between samples and

583   feature extraction. In order to yield higher consensus alignment quality of MS2 spectra to

584   improve database matching and molecular networking, the 35 samples from this experiment

585   were combined in MzMine with 756 coral reef environmental and experimental DOM samples

586   belonging to tandem studies conducted during the same fieldwork period at Gump Station.

587   Detailed chemoinformatic parameters can be found in the supplemental methods. Metabolite

588   cheminformatics generated 54,040 total metabolite ion-features (hereafter referred to as

589   features). Ten procedural blanks (LC/MS grade water run in parallel with samples) were

590   included in the run. These procedural blanks were used to identify background features and

591   transient features in the 35 samples from this experiment. Background features were defined as

592   features with an average intensity across all samples which is less than double the maximum

593   intensity of that feature in the procedural blanks. Transient features are defined as features that

594   do not exceed 5×10^4 extracted ion chromatogram values (XIC) in more than 2 samples. Blank

595   correction and transient feature removal removed 29,286 and 6,483 features, respectively. This

596   resulted in 18,271 features with XIC-values (Extracted-ion chromatogram values or peak areas)

597   which composes what we consider the exo-metabolome (mixture of ambient and exudate

598   features) which was used in downstream analysis.

599

600   *Statistics*

601   Data analysis and statistics were done using R (version 4.2.1). Main packages used are

602   the core packages within tidyverse (Wickham et al., 2019), vegan (Oksanen, 2013),

603 BiodiversityR (Kindt & Coe, 2005), pairwiseAdonis (Martinez P., 2020), and stats (R Core Team,

604 2013). The OTU co-occurrence network was generated using SPIEC-EASI (Kurtz et al., 2015)

605 and visualized using Cytoscape (version 3.9.1) (Shannon et al., 2003). R scripts and additional

606 packages are available through https://github.com/NIOZ-DOM-Analysis/ABCDom.

607 Symbiodiniaceae cell densities and bacterioplankton cell concentrations had Gaussian

608 distributions after log10 transformation and square root transformation, respectively, and

609 treatment effects were tested using ANOVAs. Surface area normalized DOC flux for the coral

610 treatments was determined by calculating the difference in DOC concentration between each

611 treatment and their respective negative controls, normalizing this value to coral surface area

612 and dividing it by the duration of the DOC exudation period (three hours). DOC areal flux data

613 had a non-Gaussian distribution and thus treatment was tested using non-parametric Kruskal-

614 Wallis tests. PERMANOVA tests were run on weighted Unifrac dissimilarity matrices derived

615 from 16S amplicon sequencing data to test the effect of treatment on microbial community

616 structure. To assess multivariate shifts in the exo-metabolomes, the metabolite feature table

617 containing XIC data was converted to relative abundance data and used to generate a Bray-

618 Curtis dissimilarity matrix, which was then used in downstream PERMANOVA testing. The

619 correlation between metabolomic and microbiota data from this experiment was statistically

620 tested using both Mantel Tests and Procrustes Tests in R (version 4.2.1) and visualized with a

621 Procrustes plot.

644 **AUTHOR CONTRIBUTIONS**

645 WJS = Wesley J. Sparagon

646 MGIA = Milou G.I. Arts

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656   CEN = Craig E. Nelson

657

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

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

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

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

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

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

664

665   **COMPETING INTERESTS**

666   The authors declare no competing interests.

667

668   **DATA AVAILABILITY**

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

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

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

672   available and deposited in the MassIVE data repository (http://massive.ucsd.edu) under the

673   accession number MSV000088021 (MassIVE repository made public upon acceptance).

674

675   **CODE AVAILABILITY**

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

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

678   upon acceptance).

679

680

681

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1086

FIGURE LEGENDS

Figure 1: Field collections and experimental design. Unbleached and bleached corals were

collected from a reef in Mo'orea, French Polynesia immediately following a bleaching event.

Picture on top: the LTER1 fore reef in Mo'orea, French Polynesia representative of the

status of the reef where both bleached and unbleached corals were present. **A.I-A.V)**

Overview of the experimental design. In addition to the four treatments two negative

controls of ambient and heated water were run in parallel but are not shown in the

overview. **A.I)** Coral nubbin collection of non-bleached and bleached corals. **A.II) 6** day

pretreatment in flow through aquaria at ambient or heated water temperatures. **A.III)** DOM

exudation (*one replicate aquaria was lost before exudation), **A.IV)** 36 hour dark bottle

incubation, **A.V)** and sampling of DNA (16S), DOC, and DOM. **B)** Mean seawater

temperatures over the period from January 1st 2018 until December 31st 2019 from three

fore reef LTER sites. Standard deviation depicted in blue. The orange line indicates the

thermal stress accumulation threshold level of 29°C (Leinbach et al., 2021; Pratchett et al.,

2013; Speare et al., 2021). Bleaching was first observed in April 2019 (Leinbach et al.,

2021), indicated by the start of the red line, which continued until the temperature levels

dropped under the thermal stress accumulation threshold. The experiment, indicated by the

purple block, was started immediately after temperatures dipped below the thermal stress

accumulation threshold. **C)** Box and whisker plot of a subset of collected nubbins from the

three coral species (*Acropora pulchra, Pocillopora verrucosa, Porites rus)* that were

sacrificed after the three day acclimatization period for symbiont cell concentration analysis

to validate the observed bleaching status at collection **D)** Box and whisker plot of the total

symbiont cell concentrations in each aquaria after seven days.

Figure 2: DOC exuded and microbial growth on exudates. **A)** Bar plots of the mean surface

1113   area normalized DOC concentrations for the four coral treatments. Error bars indicate

1114   standard error of the mean. **B)** Bacterial growth curves for the six treatments in the 36 hour

1115   bottle incubation, error bars indicate standard error of the mean. Significant differences

1116   between treatments (Tukey post-hoc test, $p < 0.05$) are denoted by the square brackets after

1117   each treatment name in the legend.

1118

1119   **Figure 3**: Changes in microbial communities in response to exudates. **A)** Non-metric

1120   multidimensional scaling of microbial community samples using Unifrac distances derived

1121   from 16S amplicon data. A dashed ellipse denotes the 3 coral stress treatments while a

1122   solid ellipse denotes the coral Control treatment. **B)** Two-way heatmap of the most

1123   abundant bacterial families in each treatment. Abundant families were defined as: relative

1124   abundance ≥ .005 in samples ≥ 3 or a relative abundance ≥ .1 in samples ≥ 1. Each cell

1125   represents the z-scored mean relative abundance of a given family in a treatment. Cells are

1126   colored according to z-score, with warmer colors indicating enrichment and cooler colors

1127   indicating depletion. Clustering was performed using Euclidian distances. **C)** Visualization

1128   of the 31 OTUs determined to be significantly differentially abudant (DA) in at least one of

1129   the three stress treatments compared to Control samples by DESeq2. Dotplot of the log2

1130   fold-change values for the 31 significantly DA OTUs in the three coral stress treatments.

1131   Each dot represents a given OTU in a given treatment. Dot height on the y-axis and color

1132   correspond to log2 fold-change values. Error bars depict the standard error of each log2

1133   fold-change value calculated by DESeq2. Dot size corresponds to mean raw abundance.

1134   Each OTU is labeled according to its class, family, and Genus_OTUNumber on the x-axis.

1135   Asterisks denote a significantly DA OTU in a treatment.

1136

1137   **Figure 4:** Compositional differentiation of coral exudates (as measured by untargeted

1138   tandem mass spectrometry) and correspondence with composition of microbial

1139   communities grown on exudates. **A)** Non-metric multidimensional scaling plot of t0

1140   metabolomic samples using bray curtis dissimilarity. A dashed ellipse denotes the 3 coral

1141   stress treatments while a solid ellipse denotes the coral Control treatment. **B)** Procrustes

1142   visualization of multivariate metabolomic and microbial samples. Arrows point from

1143   microbial samples to corresponding metabolomic samples.

1144

1145   **<u>Figure 5:</u>** Conceptual representation of biogeochemical changes during a coral bleaching

1146   event. Bleaching progresses from left to right, with SST values increasing until their peak

1147   and then return to ambient values. Corals experience a change in physiological state and

1148   symbiont densities through the thermal anomaly, going from "Healthy" to "Thermal Stress

1149   Onset" to "Peak Bleaching" and lastly, "Recovering". The associated treatment names from

1150   our experiment are written below the corals. Symbiont densities for each treatment are

1151   plotted with temperature, with densities decreasing through "Peak Bleaching" and then

1152   increasing slightly in "Recovering." Densities were derived from data presented in Figure

1153   1D. DOM flux is highest at "Thermal Stress Onset", indicated by the size of the arrows

1154   pointing from corals to "DOM". In all 3 of the stressed treatments, bacterioplankton

1155   communities shift towards a "microbialized" state marked by increased cell counts

1156   (indicated by the size of the arrow pointing towards the pie chart) and a greater relative

1157   abundance of copiotrophs and pathogens, namely in the Alteromonadaceae,

1158   Pseudoalteromonadaceae, and Flavobacteriaceae families. We propose that these

1159   microbialized communities derived from stressed coral DOM exudates further harm the

1160   corals via hypoxia from increased bacterial loads and disease from the uptick in bacterial

1161   pathogens. The state of microbialization is most pronounced at the onset of thermal stress,

1162   may push corals towards more severe bleaching and ultimately, mortality.

1163

TABLES

OTU	Heated adjusted pvalue	Bleached adjusted pvalue	Bleached + Heated adjusted pvalue	Heated l2fc	Bleached l2fc	Bleached + Heated l2fc	Phylum	Class	Order	Family	Genus
Otu01224	1.57E-06	6.00E-08	2.71E-05	9.847232822	10.79266169	8.36232019	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudoalteromonadaceae	Pseudoalteromonas
Otu01296	0.000856922	0.000561011	0.005141682	10.04404043	10.45934919	8.232520837	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudoalteromonadaceae	Pseudoalteromonas
Otu00322	6.42E-08	2.29E-09	2.21E-09	22.86585664	24.67060057	22.36474822	Bacteroidetes	Bacteroidia	Chitinophagales	Saprospiraceae	uncultured
Otu00734	8.50E-23	3.11E-22	2.80E-20	25.79903195	25.54192061	22.46096177	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonadaceae_unclassified
Otu00195	0.013386864	0.00193969	0.163719978	1.369049784	1.622337073	0.845563362	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonas
Otu00002	0.004336786	0.000715469	0.120200566	1.292770944	1.468968919	0.775714091	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonas
Otu00008	0.012939139	0.035693556	0.153825239	-1.15038439	-0.99083639	-0.723915892	Proteobacteria	Gammaproteobacteria	Cellvibrionales	Halieaceae	OM60
Otu00179	3.03E-06	0.717552218	3.63E-11	-8.977840531	1.002252708	-10.22923634	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonadaceae_unclassified
Otu00277	0.005073071	0.110479945	0.010219414	1.820452043	1.183562608	1.550819102	Bacteroidetes	Bacteroidia	Flavobacteriales	Flavobacteriaceae	uncultured
Otu00048	0.00042511	0.386129529	0.000257098	1.560964377	0.591538296	1.434128075	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Aestuariibacter
Otu00853	0.006798514	1	0.000765194	9.519537909	0	10.36647892	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudoalteromonadaceae	Pseudoalteromonas
Otu00058	0.048883543	0.931163267	0.302512595	-2.52361206	-0.482066258	-1.518716588	Bacteroidetes	Bacteroidia	Flavobacteriales	NS9_marine_group	NS9_marine_group_ge
Otu00823	NA	0.031179732	0.023655739	8.24000674	9.123083651	8.911697244	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudoalteromonadaceae	Pseudoalteromonas
Otu01012	NA	0.015381298	0.997343993	-0.587243215	-6.975738423	0.518289667	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonadaceae_unclassified
Otu01023	NA	0.015381298	0.997343993	-0.687454186	-6.963518469	0.238381381	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonadaceae_unclassified
Otu00419	NA	0.035693556	0.997343993	-1.158221028	-7.988865898	-0.928714273	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Litoricolaceae	Litoricola
Otu00327	NA	0.075398398	0.038471134	7.309356596	8.193753569	8.464131894	Euryarchaeota	Thermoplasmata	Marine_Group_II	Marine_Group_II_fa	Marine_Group_II_ge
Otu00476	NA	0.931163267	0.036816121	-0.575524572	0.963578486	-8.258405214	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	Rhodobacteraceae_unclassified
Otu00649	0.065233476	0.034948803	0.011581861	1.985756711	2.101911452	2.205220625	Proteobacteria	Gammaproteobacteria	Alteromonadales	Colwelliaceae	Thalassotalea
Otu00101	0.099973871	0.002285941	0.234525577	2.185078263	3.294200193	1.633946032	Bacteroidetes	Bacteroidia	Chitinophagales	Saprospiraceae	uncultured
Otu00181	0.69627657	0.035693556	0.825289484	0.777679188	2.221388853	0.908460509	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	Rhodobacteraceae_unclassified
Otu00027	0.502997039	0.001748299	0.245692049	-0.714321143	-1.943918868	-0.898704378	Proteobacteria	Gammaproteobacteria	Oceanospirillales	Litoricolaceae	Litoricola
Otu00410	0.520079901	0.000561011	0.997343993	-1.991835073	-8.511628793	-0.632952773	Bacteroidetes	Bacteroidia	Flavobacteriales	Flavobacteriaceae	Kordia
Otu00480	0.495008674	0.002075657	0.997343993	2.222815497	5.766700401	1.107160047	Bacteroidetes	Bacteroidia	Flavobacteriales	Cryomorphaceae	Phaeocystidibacter
Otu00075	0.116575213	0.005535059	0.068099299	2.552530067	3.699294535	2.545924273	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudoalteromonadaceae	Pseudoalteromonas
Otu00085	0.168430135	0.004035638	0.163719978	1.965130057	3.203074746	1.797279721	Proteobacteria	Gammaproteobacteria	Alteromonadales	Pseudoalteromonadaceae	Pseudoalteromonas
Otu00802	0.825080317	5.56E-10	0.997343993	1.328142611	-19.63555197	1.188804472	Proteobacteria	Deltaproteobacteria	Bdellovibrionales	Bdellovibrionaceae	OM27_clade
Otu00009	0.394038388	0.007270622	0.997343993	-1.293968348	-2.496030483	0.162912968	Proteobacteria	Gammaproteobacteria	Betaproteobacteriales	Methylophilaceae	OM43_clade
Otu00368	0.529884931	0.231526274	0.029464859	0.927913394	-1.38182967	1.855013862	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonadaceae_unclassified
Otu00457	0.805201058	0.941906395	0.000151366	-1.195502441	0.494594853	-8.927337169	Proteobacteria	Alphaproteobacteria	Rhodobacterales	Rhodobacteraceae	Rhodobacteraceae_unclassified
Otu00686	0.964756238	0.663330615	0.02552918	0.234359488	1.952445776	-4.511709297	Proteobacteria	Gammaproteobacteria	Alteromonadales	Alteromonadaceae	Alteromonas

Table 1: DESeq2 results for the 31 OTUs that were significantly differentially abundant in at least one coral stress treatment relative to coral Controls.

1165